

## Mole Cricket Hunters of the Genus *Larra* in the New World (Hymenoptera: Sphecidae, Larrinae)

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**Abstract.**—Species of *Larra* in the New World are described, illustrated, their distributions summarized on maps, and a key for their identification provided. The known biologies are summarized and past efforts to introduce exotic species to the U.S. and Puerto Rico to control mole crickets are described. Eight species are recognized including one new one, *stangei*, from Bolivia and Argentina, and they are divided among three species groups. The females of two species, *bicolor* Fabricius and *praedatrix* Strand are inseparable. The following new synonymy is proposed: *Larrada gastrica* Taschenberg, 1870, *Larra guiana* Cameron, 1912, and *Larra scapteriscica* Williams, 1928 = *Larra bicolor* Fabricius 1804; *Larra paraguayana* Strand, 1910, *Notogonia gastrifera* Strand, 1910, and *Larra pacifica* Williams, 1928 = *Larra praedatrix* (Strand), 1910; *Larra braunsii* Kohl, 1898, *Larra transandina* Williams, 1928 = *Larra godmani* Cameron, 1889 (*godmani* is the first available name for the preoccupied species *Larrada aethiops* Smith, 1873). Species groups are used to arrange the species on a world basis, and the Old World subgenus *Cratolarra* Cameron is reduced to a synonym of *Larra*. Some characters that are important from a phylogenetic standpoint are analyzed for *Larra* and the other genera in the subtribe Larrina. A cladogram showing relationships of these taxa is provided. *Larra* is demonstrated to be derived from ground nesting ancestors.

The genus *Larra* has become important in recent years because of the need to find natural enemies of three neotropical mole crickets introduced to the southeastern United States. Mole crickets cause millions of dollars of damage yearly to turf and crops, and they cannot be controlled economically with chemicals. Thus, natural enemies offer the best hope for control. Wasps of the genus *Larra* are exclusive predators of mole crickets, but the New World species have not been identifiable with any degree of certainty due to the lack of a modern revision. Furthermore, choosing the right species of *Larra* for liberation in the U.S. depends on knowledge of their distribution in the Neotropical Region and their host preferences. This revision has resolved identification of the species (although there are still problems that need further study) and mapped their geographic ranges. Determination of host preferences is beyond the scope of my study, but now that the species of *Larra* are identifiable, other scientists can examine predator/host relationships more accurately.

When this study was initiated the New World fauna was represented by 16 species of *Larra* (Bohart and Menke, 1976), all but one of which were Neotropical. After examining the types of most of these, as well as descriptions of a few taxa whose types are missing, one species, *parvula* Schrottky (1903), has been transferred to the genus *Liris* (New

Combination), and two others listed by Bohart and Menke in the genus *Liris*, *gastrifera* Strand (1910) and *praedatrix* Strand (1910), have been transferred to *Larra* (New Combination). Considerable new synonymy has resulted in reducing the number of New World species of *Larra* to eight, one of which is new to science. These species have been segregated into three species groups.

Problems of species discrimination remain. For example, the two most abundant species in the New World, *bicolor* Fabricius and *praedatrix* (Strand), are separable only in the male sex, and the latter species has considerable genitalic variation. This variation may mean that there are more species than I have recognized, but resolution of this will probably require rearing experiments, or more sophisticated techniques such as cuticular hydrocarbon analysis, not to mention more intensive collecting. In summary, *Larra* is a frustratingly difficult genus, and it is sure to tax the ability of the next person who studies it.

### INSTITUTIONS LENDING MATERIAL

I have examined over 4200 specimens during this study. They were borrowed from the following collections. Parentheses enclose the name of the contact person and capitalized symbols used to identify sources of material cited in the text.

- Academy of Natural Sciences, Philadelphia, Pennsylvania (Donald Azuma)(ANSP)
- American Entomological Institute, Gainesville, Florida (David Wahl)
- American Museum of Natural History, New York (Eric Quinter)
- Anthony Raw collection, Universidade de Brasília, Brasília D.F., Brasil
- Bee Biology Laboratory, USDA, Utah State University, Logan, Utah (Terry L. Griswold)
- Bishop Museum, Honolulu, Hawaii (Scott Miller) (BISHOP)
- California Academy of Sciences, San Francisco, California (W. J. Pulawski)
- California Insect Survey, University of California, Berkeley, California (Michael Prentice)
- California State Collection of Arthropods, Sacramento, California (Marius Wasbauer)(CSDA)
- Canadian National Collection, Ottawa, Canada (John Huber)
- Carnegie Museum, Pittsburgh, Pennsylvania (Chen Young)
- Centro de Investigación y Mejoramiento de la Caña de Azúcar, Santa Cruz, Bolivia. (Cristobal Pruett)
- Department of Entomology, Cornell University, Ithaca, New York (E. R. Hoebeke)(CORNELL)
- Florida State Collection of Arthropods, Gainesville, Florida (F. D. Bennett, Lionel Stange) (FSDA)
- Henry Hespdenheide Collection, University of California, Los Angeles, California
- Hope Entomological Collections, University of Oxford, Oxford, United Kingdom (C. O'Toole) (OXFORD)
- Illinois Natural History Survey, Champaign, Illinois (Kathleen Methven)
- Instituto Miguel Lillo, Tucuman, Argentina (A. Willink)
- Istituto di Entomologia Agraria e Apicoltura, Torino, Italy (Guido Pagliano)
- Manfredo Fritz Collection, Salta, Argentina (FRITZ)
- Martin Cooper Collection, Lyme Regis, Dorset, United Kingdom
- Martin-Luther-Universität, Halle, Germany (HALLE)
- Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (Jorge Genise).
- Museo de Invertebrados G. B. Fairchild, Universidad de Panamá, Panamá (Diomedes Quintero A.)
- Museu de Zoologia, Universidade de São Paulo, Brasil (Carlos Brandão)
- Museum d'Histoire Naturelle, Genève, Switzerland (Claude Besuchet) (GENEVA)
- Museum für Naturkunde der Humboldt-Universität zu Berlin, Germany (Frank Koch) (BERLIN)
- Museum National d'Histoire Naturelle, Paris, France (Janine Weulersse) (PARIS)
- Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (James Carpenter)
- Museum of Zoology, University of Michigan, Ann Arbor, Michigan (Mark O'Brien)
- Nationaal Natuurhistorisch Museum, Leiden, The Netherlands (Kees van Achterberg) (LEIDEN)
- National Museum of Natural History, Washington D.C. (A. S. Menke) (USNM)
- Natural History Museum of Los Angeles County, Los Angeles, California (Roy Snelling)
- Naturhistorisches Museum, Vienna, Austria (Max Fischer) (VIENNA)
- Oregon State University, Corvallis, Oregon (George Ferguson)
- Provincial Museum of Alberta, Alberta, Canada (Albert Finnermore)(ALBERTA)
- Richard M. Bohart Entomological Museum, University of California, Davis, California (Lynn Kimsey)
- Snow Entomological Museum, University of Kansas, Lawrence, Kansas (Robert W. Brooks)
- The Natural History Museum, London, United Kingdom (Colin Vardy) (BMNH)
- Universidad Central de Venezuela, Maracay, Venezuela (Jose Luis Garcia R.) (MARACAY)
- Universidad de Costa Rica, San José, Costa Rica (Paul Hanson)
- Zoological Museum, Moscow, Russia (Alexander V. Antropov)
- Zoologisk Museum, Copenhagen, Denmark (Ole Lomholdt) (COPENHAGEN)

## BIOLOGY

Bohart and Menke (1976) summarized the literature on *Larra*. Since then, a number of papers have been published on *Larra bicolor* by workers associated with the introduced mole cricket problem in Florida, principally James L. Castner. Much of this subsequent literature was summarized by Castner (1988), and the account that follows, unless stated otherwise, is taken from that paper.

### *Larra bicolor* Fabricius

**Foraging.**—Floral visitation occurs from about 8:30AM to 3:30PM with males predominating in the morning. In Puerto Rico *L. bicolor* most commonly visits flowers of *Spermacoce verticillata* L. (Rubiaceae), but *Croton glandulosus* L. and *Euphorbia heterophylla* L. (Euphorbiaceae), both of which have extrafloral nectaries, are also favorites.

In Bolivia *L. bicolor* visits *Cissus* sp. (Vitaceae) almost exclusively if it is flowering, but *Spermacoce verticillata*, *Euphorbia* sp., and occasionally *Mikania micrantha* (Compositae) are attractive to the wasp (Bennett and Pruett, 1991).

**Mating.**—Chemoreception of a female pheromone is apparently used by the male to locate the opposite sex when several meters away, but once near the potential mate, vision is used to home in on her. Females are approached from behind, the male attempting to mate by either running up on her, or flying directly on to her. Castner (1988) stated that females foraging on flowers are never approached, and that only females on the ground were mated, but Bennett and Pruett (1991) commonly observed males searching for females in foliage.

Actual mating has rarely been observed. According to Bennett and Pruett (1991), once a male has landed on a female, she raises her abdomen if

she is receptive, and the male engages her for less than five seconds ("... it is almost a non-event"). Afterwards both individuals groom the tip of the abdomen with their hindtarsi.

*Prey searching.*— This activity occurs from about an hour after sunrise to 3:45 PM. Prey searching occurs on cloudy, overcast days as well as sunny ones, but not apparently on rainy days. Typically the female walks over the ground until a mole cricket surface gallery is encountered, whereupon she excavates down into it and enters the tunnel. Just what happens between wasp and mole cricket in the burrow is unknown, but the orthopteran typically evades the wasp by surfacing. According to Castner, surfacing mole crickets escape capture by the wasp about 50% of the time. Wasps return to the surface often apparently to determine if the host has surfaced. Small nymphs are attacked as well as large adults.

*Paralysis of prey.*— The female captures the surfaced mole cricket. She then stings the host repeatedly in a fixed pattern: to the base of the fore and midlegs, and to the base of the palpi. Paralysis generally lasts for 3 to 4 minutes. If the cricket revives before oviposition is complete, more stings are administered. Once the mole cricket is paralyzed, the wasp often turns it on its back and chews at the base of one of the forelegs, appearing to feed on exuding body fluid.

*Oviposition.*— Prior to oviposition the wasp usually rubs the tip of her abdomen over the ventral area of the mole cricket, possibly to determine if a wasp egg or larva is already present. If an egg is detected, the wasp initiates a searching/biting behavior that may take several minutes before the egg is removed (Castner, 1986). In experiments females would even remove their own eggs from mole crickets. The egg is attached in the soft, membranous tissue between the first and second pair of legs of the host, lateral to the midventral line. After deposition of the egg, the wasp then either flies away or remains with the host until it revives and re-enters the ground. Some wasps have been observed to chase away foraging ants.

*Larval development.*— Under laboratory conditions eggs hatch in 6-7 days. The first instar larva feeds on hemolymph at the site of egg attachment and after 8-9 days has progressed through four instars, growing slowly all the while. One to three days later the fifth and final instar has killed the host, consumed the soft, inner tissues and grown suddenly to a length of 14-26 mm. In about a day the mature larva spins a cocoon in the mole

cricket's gallery. An adult wasp emerges 6-8 weeks later.

*Host suitability.*— *Larra bicolor* is not necessarily host specific, at least under laboratory conditions in Florida, where the wasp was able to develop on five neotropical species of *Scapteriscus* mole crickets (*abbreviatus* Scudder, *borelli* Giglio-Tos (*acletus* Rehn and Hebard is a synonym, see Nickle 1992), *vicinus* Scudder, *didactylus* (Latreille), and *imitatus* Nickle and Castner), the first three of which are established in the state. However, survival on *S. didactylus*, an exotic species so far not known in the U.S., was significantly less than in the other four, suggesting possession of some type of anti-parasite mechanism by the host. Similar results were obtained in laboratory tests in Bolivia with four species of *Scapteriscus* (Pruett and Bennett, 1991), but *bicolor* preferred *S. vicinus* Scudder. In laboratory studies, *L. bicolor* reluctantly accepted the native Floridian mole cricket *Neocurtilla hexadactyla* (Perty), whose range also includes much of South America (Castner, 1988, Pruett and Bennett, 1991). But this mole cricket has a defense mechanism: it secretes a viscous anal fluid that entangles the attacking wasp, thus permitting the prospective host to escape. In Bolivian laboratory trials, Pruett and Bennett demonstrated that of 328 *bicolor* eggs successfully laid on *N. hexadactyla*, only 5 developed to the pupal stage, and many died in the first instar. Apparently this mole cricket has more than one mechanism for dealing with its attackers.

#### *Larra analis* Fabricius

Smith (1935) extensively studied the only native North American *Larra*, and his account shows that *analis* has basically the same behavior as *bicolor*. This wasp attacks *Neocurtilla hexadactyla*, the native North American mole cricket. Smith observed that wasps sometimes were entangled by the same sticky substance that this mole cricket used to thwart attacks by *bicolor*. The only difference in the behavior of *analis* is that the egg is attached behind the hindleg. Development from egg to cocoon ranged from 12 days in mid summer to about 30 days in the fall.

Egg placement behind the hindleg was noted by Williams (1928, p. 42) in an unidentified species from Tena, Ecuador. The only species from Tena represented by females in Williams' material (BISHOP & USNM) are *godmani* (Cameron) and *altamazonica* Williams, both of which belong in the *analis* species group. Egg placement behind the

hindleg of the host may thus be a feature of the *analis* group.

#### *Larra godmani* Cameron

Two females that I have studied, one from Chapare, Bolivia, and one from Cauqueta, Colombia, have prey pinned beneath them. Both are immatures of a species of *Neocurtilla* (det. D. Nickle). Bennett et al. (1990) state that in Bolivia this *Larra* (as *braunsii*) attacks medium to large nymphs of *Scapteriscus vicinus* and small nymphs of *S. borellii* (as *acletus*).

### INTRODUCTIONS TO CONTROL MOLE CRICKETS

**Hawaii.**—Introductions of exotic mole crickets to Hawaii, Puerto Rico, and the southeastern US prompted a search for control agents. F. X. Williams pioneered the research on *Larra* as a control agent. He explored the Philippines and Australia in an effort to find natural predators for *Gryllotalpa africana* (Palisot de Beauvois), established on the islands of Oahu and Kauai. In 1921 and 1925 he sent live material of *Larra luzonensis* Rohwer collected in the Philippines to Hawaii, and it was liberated at various sites on Oahu where it became established (Williams, 1928). He also liberated another Philippine species, *L. amplipectus* (Smith) (as *L. sanguinea*), in 1922 but it failed to become established.

Williams then turned to South America in his search for an effective species of *Larra*. He sent material of *Larra bicolor* (as *americana* and *scapteriscica*) taken in Belém, Brasil, to Hawaii in 1924, but the introduction failed.

**Puerto Rico.**—George Wolcott (1941) sought predators of mole crickets at Belém, Brasil, where F. X. Williams (1928) found *Larra* to be common. Between 1936 and 1940 Wolcott and his associates liberated a number of collections of *L. bicolor* in Puerto Rico, and the species became established there. Of particular interest was the discovery that survival of live wasps in transport was greatly enhanced when live but paralyzed mole crickets accompanied them. This technique resulted in the accidental introduction to Puerto Rico of another species of mole cricket, however (Nickle & Castner, 1984).

**Florida.**—Three exotic species of mole crickets of the genus *Scapteriscus* were introduced into the southeastern U.S. around the turn of century

(*abbreviatus*, *borellii*, and *vicinus*). Now well established, they cause considerable damage to turf and pasture grasses, especially *vicinus*. It is estimated that in Florida alone these herbivores cost in excess of \$44 million annually when damage and control measures are tallied (Hudson, et al., 1988).

In the late 1970's scientists at the University of Florida began investigating potential predators and parasites, and by 1981 had released *Larra bicolor* from Puerto Rico at three sites in Florida: Gainesville, Tampa, and Fort Lauderdale (Hudson, et al., 1988). Subsequent releases were made at Bradenton and Lakeland in 1982-83. The wasp became established only at Fort Lauderdale, presumably either because the other sites were too cold for winter survival of an essentially tropical wasp, or because too few wasps were released or they were too old. Currently searches for suitable *Larra* for introduction to northern Florida have been centered in Bolivia. Bolivian material of *L. bicolor* and *L. godmani* (as *braunsii*) was liberated at several sites in Alachua Co. in 1988-89 (Bennett et al., 1990). The success of these releases has not been evaluated.

Among material of *L. bicolor* assembled for this revision is a single female collected at Watson's Hammock, Big Pine Key in Monroe Co., Florida, in 1986 (ALBERTA). This site is far from Fort Lauderdale, and it may represent a hitherto undetected natural population of *L. bicolor*, or a chance introduction. As pointed out in the systematic treatment of this species, it is possible that this Big Pine Key female is actually the species *L. praedatrix*.

### RECOMMENDATIONS FOR INTRODUCING LARRA TO FLORIDA

The three introduced mole crickets in the southeastern U.S. originated in southern South America, primarily the region around Buenos Aires, Argentina (Nickle and Castner, 1984). Thus it would seem most rewarding to collect *Larra* from that region for introduction to the U.S. Also, the climate there is temperate, rather than tropical, and the wasps would have a better chance of surviving in North America, especially if collected south of the 30th Parallel. Four species of *Larra* occur commonly in the area around Buenos Aires: *burneiseri*, *bicolor*, *praedatrix*, and *princeps* (the last three belong in the *bicolor* group). Any of these species may be good candidates for introduction to Florida, and in fact, *L. bicolor* from Puerto Rico has been successfully



introduced there. It survived only in southern Florida, however, and introductions of *L. bicolor* from a more temperate region such as northern Argentina would seem more logical. Prey specificity for species of *Larra* is poorly understood at present, and the mole crickets attacked by *burmeisterii*, *praedatrix*, and *princeps* are unknown. *Larra princeps* in particular would seem worthy of study, because it has the southernmost range in South America of any species in the genus (nearly to the 40th Parallel) and thus may be expected to survive in the cooler parts of the southeastern U.S.

#### Genus LARRA Fabricius

*Larra* Fabricius, 1793:220. Type species: *Larra ichneumoniformis* Fabricius, 1793 (= *Sphex anathema* Rossi, 1790), designated by Latreille, 1810.

*Larrana* Rafinesque-Schmaltz, 1815:124. Emendation of *Larra* Fabricius.

*Lara* Drapiez, 1819:54. Lapsus or emendation of *Larra* Fabricius. *Monomatium* Shuckard, 1840:181 (no species). Type species: *Laraxena princeps* F. Smith, 1851, designated by Pate, 1935 (first included species).

*Lyrops* Dahlbom, 1843:132. Type species: *Tachytes paganus* Dahlbom, 1843, monotypic. Not *Lyrops* Illiger, 1807.

*Laraxena* F. Smith, 1851:30. Type species: *Laraxena princeps* F. Smith, 1851, monotypic.

*Larrada* F. Smith, 1856:273. Type species: *Larrada anathema* (Rossi), 1790, original designation.

*Cratolarra* Cameron, 1900:34. Type species: *Cratolarra femorata* Cameron, 1900, monotypic. NEW SYNONYM.

The extensive generic description in Bohart and Menke (1976) is generally quite thorough, but one structure was insufficiently described, and two others not mentioned. The female scape was described as conspicuously shining in contrast to the flagellum in many species, and while that is true, it is important to add that it is also largely asetose and impunctate in those species (Fig. 8). The pronotum in *Larra* usually has a transversely elongate sulciform depression anteromedially, although in some species there are two oval pits in the same position that may be narrowly joined. Finally, in many species of *Larra*, the inner surface of the forebasitarsus has an asetose linear polished zone (Fig. 28). It occurs in both sexes but is best developed in the female. In a few species the basitarsus is setose throughout (Fig. 26) as in *Liris*, or has a small, rather poorly defined asetose area (Fig. 27).

The difficulty in separating *Larra* from the genus *Liris* was well documented by Bohart and Menke (1976:235, 240). The polished, asetose zone present

on the inner surface of the forebasitarsus of many species of *Larra* is an additional difference from *Liris*, but unfortunately it is not universal. The apparent differences in the biology of these taxa argue for maintaining *Larra* as a separate genus, but the problem of finding clear morphological differences remains.

*Subgenera and species groups.*—Bohart and Menke (1976) recognized two subgenera that were differentiated by the presence (*Larra*) or absence (*Cratolarra*) of spine rows on the foretibia. After examining 25 of the 60 species in the genus I have reached the conclusion that *Cratolarra* is only one of several recognizable groups within *Larra*, and certainly no more distinct than the others. My phylogenetic analysis confirms this and therefore I am synonymizing *Cratolarra* (NEW SYNONYM). I am using species groups to segregate the taxa of *Larra*. The Old World *Cratolarra* becomes the *maura* group, its name based on the oldest species in the group. Tsuneki (1967) called it the *carbonaria* group. Other Old World groups recognized by me include the *amplipennis* and *anathema* groups. The New World species are divided among the *bicolor*, *burmeisterii*, and *analis* groups. They are characterized later in the paper.

The *amplipennis* group includes species with a setose forebasitarsus, a setose female pedicel, a largely asetose polished frons in the female (an apomorphy), a flat non-beveled labrum, spine rows on the female foretibia (an apomorphy), and placoids on most flagellomeres of the male. In addition the female lacks an ocular sinus. Species examined from this group include *amplipennis* (Smith) and *betsileia* Saussure.

The *anathema* group shares most of the characters of the *amplipennis* group. But the female pedicel is largely asetose and polished dorsally, and the forebasitarsus has a poorly defined asetose zone on its inner surface; both are apomorphies. I have examined *anathema* (Rossi) and *melanocnemis* Turner. The last species is only provisionally assigned to the group.

The *maura* group lacks spine rows on the female foretibia, a character that sets it apart from all other species of *Larra*. I regard this state as plesiomorphic in *Larra* but my phylogenetic analysis suggests that in the *maura* group the absence of spines is a reversal (see Cladogram). The female pedicel is completely asetose and polished, the female frons is asetose and polished, the female upper interocular distance is less than half the lower interocular distance, and

the female vertex has a deep sinus around the inner eye margin - all apomorphies. In addition, the labrum is flat, not beveled apically, and the male has placoids on most flagellomeres; both are plesiomorphic features. Species of this group that I have examined are: *carbonaria* (Smith), *femorata* (Saussure), *fenchihuensis* Tsuneki, *heydenii* Saussure, *huzonensis* Rohwer, *maura* (Fabricius), *outeniqua* Arnold, *polita* (Smith), *saussurei* Kohl, and *variipes* Saussure.

*Species characters.*— New World *Larra* have exasperatingly few characters. Some of those used by Williams (1928) such as thoracic punctation, presence or absence of a median carina on the propodeal dorsum, body and wing color, and details of the female vertex are unreliable. Other features used by Williams are really group characters: female pedicel asetose, polished, and female vertex with ocular sinus. He was unaware of the value of placoid distribution on the male antenna as a species character for members of the  *analis*  group. On the other hand Williams used male genitalia and I have found them to be very important in the *bicolor* and *burmeisterii* groups. The genitalia of species in the  *analis*  group seem identical. The genitalic variability observed in some *bicolor* group species is perplexing and needs further study. The shape of the female pygidial plate is diagnostic for some species.

I have compared the upper interocular distance (UID) to the lower interocular distance (LID), but there is considerable variability in some species (20+ specimens measured on average) and overlap between some species. I made my measurements with an ocular micrometer at a magnification of 50X. Figures 1-4 illustrate how these measurements are made, and proper head orientation. Williams (1928) used the lengths of the pedicel and flagellomeres I-II and compared them to the upper interocular distance, but they are not any more reliable or meaningful than UID/LID comparisons.

*Character analysis.*— In order to assess the relationships of the species involved in this study, and the position of *Larra* itself within the Larrinae, I have attempted to polarize a number of characters. My outgroup consisted of the other genera of the subtribe Larrina: *Liris*, *Dalara*, *Paraliris* and *Dicranorhina*, although I have sometimes referred to taxa in the subtribe *Tachytina*. Bohart and Menke (1976) regarded *Larra* as the most primitive member of the subtribe Larrina, and *Paraliris* and *Dicranorhina* as the most derived. That may be true, but I think

that I can now demonstrate that some character states regarded by Bohart and Menke as plesiomorphic in *Larra* are really apomorphic.

In my analysis 0 = the plesiomorphic state, and 1 and 2 = apomorphic states (and do not necessarily represent transformation series). Characters 14-17 were not used in the phylogenetic analysis because they do not appear to be particularly informative, but they are included here because they may merit further study.

1. *Labrum*: 0 = flat, not broadly beveled or sloping down at apex, not emarginate; 1 = surface sloping down at apex, or broadly beveled there, free margin arcuate, obtusely angular, or lobate.

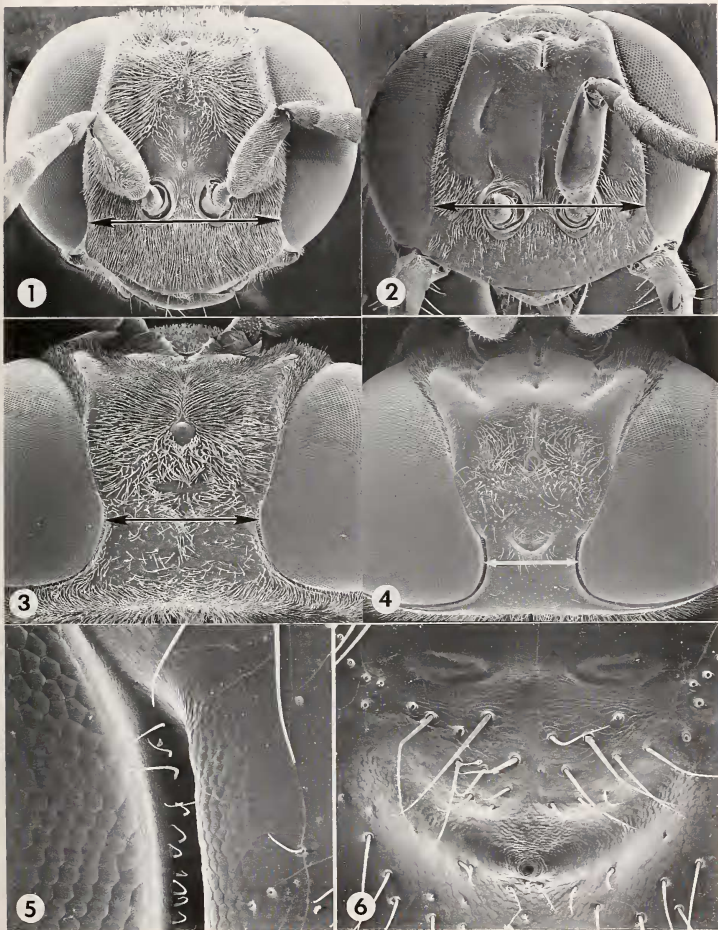
The plesiomorphic state is apparently universal in the outgroup, in all Old World *Larra*, and the monotypic *burmeisterii* group (Fig. 15) in the New World. The apomorphic state is present (Figs. 16-18, 55) in the *bicolor* and  *analis*  groups of *Larra*, both restricted to the New World. In the single species of *Paraliris* available, the labrum is flat, but the free edge is quite thick, and in *Dicranorhina* and some *Liris* the labrum has an apical emargination. These represent other apomorphic states. In the *Larra bicolor* and  *analis*  groups it is my assumption that the labrum has become elaborated to aid excavating.

2. *Female antennal pedicel*: 0 = surface densely setose, similar in appearance to flagellomeres; 1 = dorsum sparsely setose, or asetose, remainder densely setose; 2 = surface largely asetose, polished, contrasting with setose flagellum.

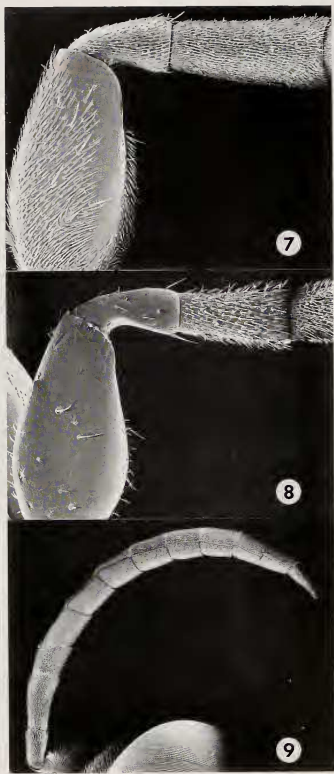
The plesiomorphic state appears to be universal in the outgroup, as well as in the New World *bicolor* group (Fig. 7) and the Old World *amplipennis* group of *Larra*. The apomorphic state is universal in the Old World *maura* group, as well as in the *burmeisterii* and  *analis*  groups (Fig. 8). The pedicel of two Old World *Larra* is intermediate. In the Australian species *L. melanocnemis* Turner, the pedicel is more or less asetose dorsally but setose elsewhere. In the Palearctic species *L. anathema* (Rossi) it is sparsely setose dorsally, and densely setose elsewhere.

3. *Placoids of male flagellum*: 0 = present on all but the first one or two flagellomeres; 1 = present on only a few flagellomeres; 2 = absent.

In the majority of the species of *Liris* examined, placoids are present on flagellomeres II-XI. Exceptions occur in the subgenus *Motes*, where some species have only a single placoid, and others have a full complement. In *Larra* all species have the plesiomorphic condition (Fig. 9) except members of the  *analis*  group (Figs. 13, 59-62). The



Figs. 1-6. Head details of *Larra*. 1-2, Face showing how to measure lower interocular distance and orientation when doing so. 1, Male of *bicolor*. 2, Female of *altamazonica*. 3-4, Top of female head showing how to measure upper interocular distance and proper orientation. 3, *bicolor*. 4, *godmani*. 5-6, Details of female vertex of *godmani*. 5, Ocular sinus along orbit of left eye. 6, Depression behind hindocelli showing pore at bottom.



Figs. 7-9. Antennal features of *Larra*. 7-8. Left female scape, pedicel, and flagellomere I. 7, *bicolor*. 8, *altamazonica*. 9. Right male antenna of *bicolor*.

intermediate apomorphic state occurs in the latter group and *Dalara*. The most apomorphic state occurs only in *Paraliris* and *Dicranorhina*. Bohart and Menke (1976) regarded the absence of placoids as plesiomorphic in the Larrinae, but in the subtribe Larrina I think the most logical assumption is that presence of placoids on most flagellomeres is the

plesiomorphic condition, and that loss of placoids is the apomorphic condition - a reversal. This is supported by the fact that species and genera in which reduction or complete loss of placoids has occurred are recognizable as derived by other character states. For example, the *analisis* group, which has only 2 to 4 placoids, has an apomorphic labrum, female pedicel, female orbital sinus, and female foretibial carina.

4. *Orbital sinus*: 0 = absent; 1, present, narrow, 2, present, broad.

A deep sinus around the upper orbit of the eye, especially in the female, is apparently absent in the outgroup as well as many species of *Larra*. A narrow sinus is usually present in the female of the monotypic *burmeisterii* group (Fig. 49). All members of the *analisis* group and the Old World *maura* group have a broad, deep sinus (Fig. 4). It is best developed in the female but is present in males as well. The function of this depression (Fig. 5) is unknown.

5. *Female frons*: 0 = dull, setose; 1 = polished, largely setose; 2 = polished, largely aetose.

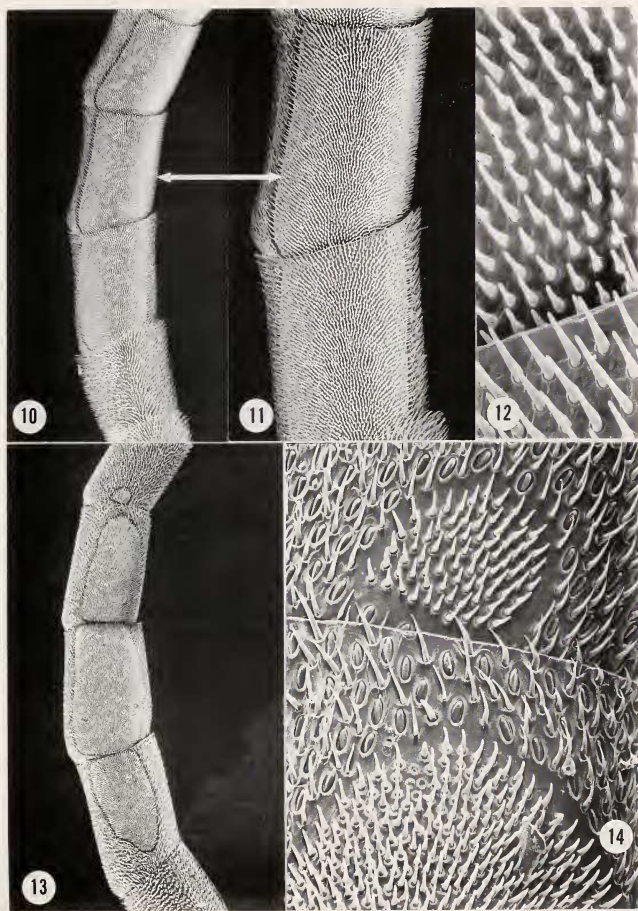
In the outgroup the frons beneath the transverse swelling is usually covered fairly densely with setation that obscures the integument which is usually dull. In nearly all female *Larra* the frons is aetose or nearly so (Fig. 2), the integument easily visible and polished. I regard this as an apomorphy. In the *Larra bicolor* group the frons is setose at least laterally (Figs. 39-40) but the integument is shiny - this represents an intermediate condition.

6. *Female mandible*: 0 = cutting edge with one or two subbasal teeth; mandible strongly arched from base to apex, outer surface somewhat angled in cross-section, narrow distad of posterobasal notch and attenuate to apex (pick-like); 1 = cutting edge without teeth; outer surface evenly curved in cross-section, broad beyond posterobasal notch almost to apex (scoop-like).

Bohart and Menke (1976, p. 224, 243) considered absence of teeth on the cutting edge to be plesiomorphic in *Larra*, but I believe that this state is apomorphic since teeth are nearly universally present in the outgroup, one exception being the subgenus *Motes* of *Liris*. Teeth are also absent in the specialized genus *Parapiagetia*, and some specialized species of the genera *Gastrosericus* and *Tachysphex* (all subtribe *Tachytina*). I hypothesize that teeth have some function in prey transport, and because female *Larra* do not carry their prey, they have lost the teeth.

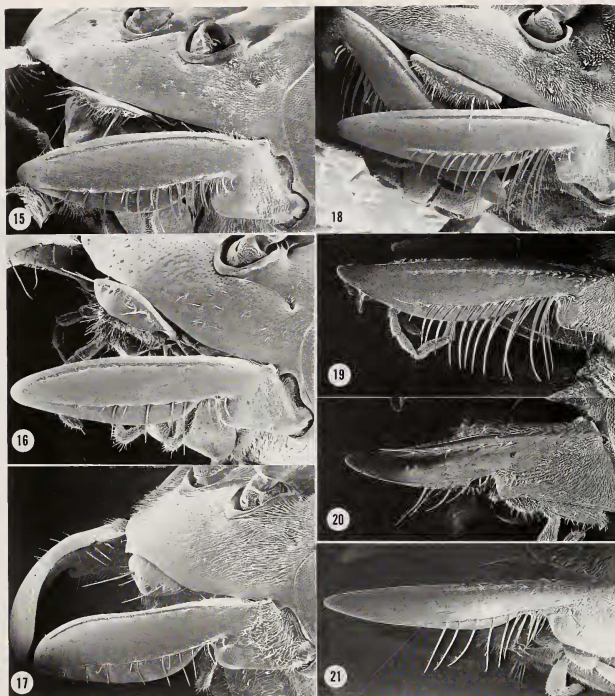
The overall form of the mandible is most often pick-like in the outgroup (Figs. 20-21), but in *Larra*





Figs. 10-14. Male flagellar details of *Larra* showing placoids. 10-12, *L. bicolor*. 10, Flagellomeres II-V with placoids on III-V. 11, Flagellomeres IV-V. 12, Setal structure of placoids on flagellomeres IV-V. 13-14, *L. analis*. 13, Flagellomeres II-VI showing placoids on III-VI. 14, Setal structure of placoids on flagellomeres V-VI.





Figs. 15-21. Details of female mouthparts in *Larra* and *Liris*. 15-18, Clypeus, labrum and left mandible in *Larra*. 15, *burmeisterii*. 16, *altamazonica*. 17, *godmani*. 18, *bicolor*. 19-21, Left mandible. 19, *Larra stangei*. 20, *Liris niger*. 21, *Liris bembesianus*.

it is often a broad, scoop-like structure (Figs. 15-17) that I hypothesize has evolved in response to their habit of simply digging down into mole cricket burrows that generally are in damp soil. Presumably the scoop form offers a more efficient digging implement than a spike-like mandible. Similar scoop-like mandibles occur occasionally in *Liris* and elsewhere in the subfamily Larrinae. Widening of the area beneath the condylar groove (Michener and Fraser 1978) contributes to the formation of the scoop in some *Larra* (Figs. 15-17).

7. *Mandibular notch*: 0 = present, located near middle of mandible; 1 = present, located close to

mandible base; 2 = reduced to small V or absent.

The function of the mandibular notch is unknown. I (Menke, 1988) came to the conclusion that the absence of a mandibular notch is plesiomorphic in the subfamily. This is clearly the generalized condition in the entire family Sphecidae. However, within the Larrinae notchless mandibles are common only in a few taxa; some examples are: *Solierella* (Miscophini), most Crabronini, *Oxybelus* (Oxybelini), and *Pison* and *Trypoxylon* (Trypoxylini). Complicating the hypothesis are the apparent reversals scattered through the Larrinae. The notch seems to have been

reduced or lost in various specialized taxa; examples are found in *Liris*, *Gastrosericus*, *Holotachysphex*, and *Tachytes*. Clearly the notch in Larrinae needs further investigation. In most members of the outgroup, as well as most genera of Larrinae, the notch is located near the middle of the mandible (Fig. 20), or slightly more basal. In *Larra*, however, it is clearly subbasal (Figs. 15-19), due in part to lengthening of the outer part of the mandible. I hypothesize that this has enhanced development of the mandible's scoop-like form. Some *Liris* with well developed tarsal rakes have elongate mandibles and the notch in these is subbasal (Fig. 21). The mandibular notch is just a small obtuse V in *Liris* subgenus *Liris*, and in one species of *Paraliris*, or is absent just as in *Dalara* and most *Paraliris*. The mandible of the latter two genera is otherwise specialized (shape, and extra teeth) which suggests to me that the absence of a notch is a loss feature (apomorphic) in Larrina. The reduction in *Liris* (*Liris*) is interpreted similarly.

8. *Setae of condylar groove of female mandible*: 0 = setae fine, not particularly stiff, not clearly rake-like (Fig. 20); 1 = setae numerous, thickened, stiff, forming a rake (Figs. 18-19, 40); 2 = setae weak, scattered, rake poorly developed (Figs. 15-17).

In most *Larra* the setae in the condylar groove (Michener and Fraser 1978) are numerous, thickened and stiff, forming a rake. Presumably it aids in digging. In the New World *analisis* group the rake setae are widely spaced and rather short (Figs. 16-17). Presumably this condition is a reversal since some species in this group have a well developed scoop-like mandible. Generally in the outgroup the setae are finer and appear less effective as a rake. There are exceptions in *Liris* (Fig. 21), some species of which excavate very deep nests.

9. *Apex of female mandible*: 0 = simple; 1 = bidentate.

A simple apex is the ground plan condition in the subtribe Larrina, and indeed in the family Sphecidae. However, the apex is bidentate in the female of *Dalara* and in both sexes of *Paraliris* (exceptional males of one species lose the condition - see van der Vecht, 1981), an obvious apomorphy. At least one species of *Liris*, *tenebrosus* (Smith) from South America, also has a bidentate female mandible, but this is not the ground plan in this very large genus.

10. *Female foretibial spine rows*: 0 = absent; 1 = one row present; 2 = two (Fig. 23) or three present (Fig. 22).

In the outgroup the foretibia does not have a

row of stout setae except in *Liris* s.s., a few species of which, principally the non-insular taxa, have a single row. On the basis of other features, the subgenus *Liris* is a highly evolved lineage, and the foretibial setal row is apparently an apomorphic trait. The African species, *Liris* (*Leptolarra*) *croesus* (Smith), has two rows of setae, one of which consists of two or three setae. Presumably the spine rows aid in excavating; all *Liris* with them have well developed foretarsal rakes.

In *Larra* the Old World *maura* group lacks spine rows, but in the rest of the genus there are two or three rows. Commonly specimens of the *bicolor*, *burmeisterii* and *analisis* groups actually have three rows, the innermost one closely paralleling the next and consisting of two to four somewhat finer spines (Fig. 22). Because the rare occurrence of one or two spine rows in *Liris* is obviously not the ground plan condition in that very large genus, it has been omitted from the phylogenetic analysis. Thus in the analysis, condition 1 represents the presence of 2 or 3 spine rows as in *Larra*.

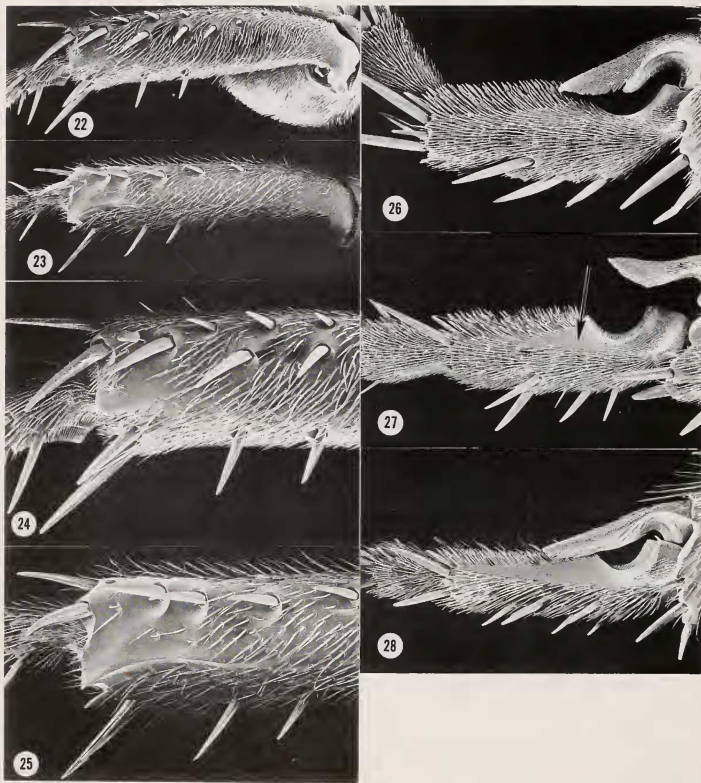
11. *Female foretibial carina*: 0 = absent (Fig. 24); 1 = present (Fig. 25).

In the outgroup and most *Larra* the outer apex of the tibia lacks a carina. In the *analisis* and *burmeisterii* groups however, there is a carina adjacent to the smooth, asetose zone at the apex. I regard this as an apomorphy.

12. *Female forebasitarsal asetose zone*: 0 = absent (Fig. 26), 1 = present (Fig. 27); 2 = present, extending to apex of segment (Fig. 28).

In the outgroup and in the *Larra amplipennis* group the basitarsus is setose within. Also one species in the *Larra bicolor* group, *stangei*, has an entirely setose forebasitarsus (Fig. 26). In the remaining groups of *Larra* the inner surface of the basitarsus distad of the basal cleaning notch has an impunctate asetose zone of variable length. This zone is a polished strip that attains the apex of the segment in the *burmeisterii*, *analisis* and *maura* groups (Fig. 28). I regard this as the most derived state. An intermediate state is found in the *bicolor* and *anathema* groups (Fig. 27), although one species in the *bicolor* group, *stangei*, exhibits the plesiomorphic condition.

13. *Biology*: 0 = captures and paralyzes prey, places prey in previously constructed nest cell and then lays an egg; 1 = temporarily paralyzes host, deposits egg, then flies away, host revives and re-enters burrow, host's burrow functioning as chamber for wasps' pupa.



Figs. 22-28. Details of left front tibia and basitarsus of female *Larra*. 22-23, Outer surface of tibia. 22, *bicolor*. 23, *godmani*. 24-25, Outer surface of tibial apex. 24, *bicolor*. 25, *godmani*, showing carina. 26-28, Inner surface of female basitarsus. 26, *stangei*. 27, *bicolor*, arrow points to asetose zone. 28, *godmani*.

Bohart and Menke (1976, p. 2, 227, 237) considered the parasitoid-like biology of *Larra* to be among the most primitive in the Sphecidae. I think however, that a different hypothesis can be made, one that results in *Larra*'s biology being considered apomorphic in *Larrina*. I propose that *Larra* has

abandoned the nest preparation habit of its ancestors, and adopted the burrow of its mole cricket host as its nest. Female morphology supports this hypothesis. A pygidial plate is used by larrine wasps as a tamping device during nest closure. *Larra* has a pygidial plate, but has no apparent use

for it because these wasps have no nest to seal. I think the plate in *Larra* is a relic from its nest building ancestors. The only excavating that *Larra* does is digging into the burrow of the mole cricket host. I hypothesize that the scoop-like mandible and mandibular rake setae common to most female *Larra* evolved to make them more efficient diggers. The spine rows on the foretibia of many *Larra* presumably have a similar explanation. Outgroup members, all of which, so far as known, transport prey after paralysis, have teeth on the cutting edge of the mandible (*Liris* subgenus *Motes* an exception) that presumably aid in grasping prey. *Larra*, which does not transport prey, has lost these teeth. The biology of the outgroup is still fragmentary or unknown except in *Liris*, and even here only a few of the nearly 300 species have been observed (Bohart and Menke, 1976, Kurczewski and Spofford, 1987). But this small data base suggests that the ground plan for the subtribe *Larrina* is for females to use pre-existing burrows or cavities for nest sites. Morphologically derived taxa like *Dicranorhina* excavate new burrows that may be maintained for several generations. Excavated burrows may be very deep as in *Liris* subgenus *Liris*.

The egg of *Larra*, at least in some Old World species, is much smaller in comparison to the size of the wasp (1.75 mm for egg, 16-19 mm for wasp) than in *Liris*, and is glued along most of its linear length to the host, presumably to prevent dislodgement by the mole cricket (Williams, 1928:38), rather than at one end as in other *Larrina*. If these two traits are apomorphies, they would support my thesis that the biology of *Larra* is specialized, rather than primitive. Egg size apparently is not always comparatively small, however, since Castner (1988) states that eggs of *Larra bicolor* are 4.0-4.5 mm long (female wasps range in size from 9.5-20 mm). Also it is not clear from published accounts that *Larra* eggs are never attached only by one end to the host.

The following characters were not used in the phylogenetic analysis.

14. *Vertex*: 0 = Upper interocular distance more than half as wide as lower interocular distance; 1 = UID less than half as wide as LID.

Both states occur in *Larra* as well as most of the outgroup. Narrowing of the UID is regarded by sphecoid workers as an apomorphy in the family. State 1 occurs occasionally in the *bicolor* and *burmeisterii* groups too. The apomorphic condition predominates in the *analisis* group and the Old World

*maura* group, both of which have a well developed orbital sinus, another apomorphy. Because of overlap between the two states in nearly each species group of *Larra*, this character is not particularly informative. Nevertheless, trends are apparent in some groups.

The vertex has a central U or V-shaped depression just behind the hindocelli which contains a pore-like opening that may have a glandular function (Fig. 6).

15. *Pronotal pit (-s)*: 0 = transversely elongate; 1 = two transversely elongate pits present that are narrowly separated; 2 = two oval pits present.

1 (Menke, 1988) demonstrated that the presence of some kind of pit or pits on the pronotal midline anteriorly was an apomorphy in Sphecidae. In the *Larrina* three basic conditions can be defined. The common one in the outgroup is a single, transversely elongate sulcus, but a pair of elongate pits occurs in *Dalara* and some *Liris*, particularly the subgenus *Liris*, although also in a few species of the subgenus *Leptolarra*. In some *Dicranorhina* there are two pits narrowly joined by a bridge. All Old World *Larra* that I have examined have a single, transversely elongate sulcus and so do most members of the New World *bicolor* group. The *analisis* and *burmeisterii* groups have a pair of separate oval pits (narrowly joined in one species). Polarization here is obviously a difficult decision but I am hypothesizing that paired oval pits is the most derived state in *Larrina*.

16. *Submarginal cell of forewing*: 0 = four sided, 1 = three sided, the inner and outer veinlets joining forming a petiole that reaches the marginal cell (Fig. 45).

Petioloation of submarginal cells is widely regarded as a specialization in Sphecidae. All members of the outgroup have the plesiomorphic state, but at least two species of *Larra* display the apomorphic condition (*princeps* (Smith) and *dux* (Kohl)).

17. *Color of abdomen*: 0 = black, 1 = red and black, 2 = red.

A black abdomen (and body in general) is the common state in the outgroup. Some species of *Dicranorhina*, one of the more specialized genera in the subtribe *Larrina*, have red color on parts of the body. In the large genus *Liris*, red occurs in very few species and is usually confined to the legs, but *rubricatus* (Smith), *rubellus* (Smith) and several others, have a red abdomen. Thus black seems to be the ground plan state, and red a derived condition. A black abdomen is apparently universal in the

Table 1. Data matrix for species groups of *Larra* and other genera of subtribe Larrina.

Taxa	Characters												
	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Dicranorhina</i>	0	0	2	0	0	0	0	0	0	0	0	0	0
<i>Paraliris</i>	0	0	2	0	0	0	2	0	1	0	0	0	0
<i>Dalara</i>	0	0	1	0	0	0	2	0	1	0	0	0	0
<i>Liris</i> ( <i>Liris</i> )	0	0	0	0	0	0	2	0	0	0	0	0	0
<i>Liris</i> ( <i>Motes</i> )	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Liris</i> ( <i>Leptolarra</i> )	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Maura</i> group	0	2	0	2	2	1	1	1	0	0	0	2	1
<i>Amplipennis</i> group	0	0	0	0	2	1	1	1	0	1	0	0	1
<i>Anathema</i> group	0	1	0	0	2	1	1	1	0	1	0	1	1
<i>Analís</i> group	1	2	1	2	2	1	1	2	0	2	1	2	1
<i>Burmeisterii</i> group	0	2	0	1	2	1	1	1	0	2	1	2	1
<i>Bicolor</i> group	1	0	0	0	1	1	1	1	0	2	0	1	1

*Larra maura* group, although some species have red legs. A mixture of black and red occurs in the *amplipennis* and *anathema* groups but I have not seen many species. *Larra melanocnemis* probably belongs in the *anathema* group and it is completely black. In the New World, an all red abdomen predominates in the *bicolor* group although one species has occasional melanic forms. In the other two New World groups the abdomen varies from black to red or a mixture of the two with some species having melanic forms. Color changes may be environmentally induced so the usefulness of color in the phylogeny of *Larra* is limited.

#### PHYLOGENETIC ANALYSIS AND RESULTS

The characters and taxa summarized in the data matrix (Table 1), were analyzed using the Hennig86 cladistics program (version 1.5) of Farris (1988). Character 8 was run unordered. Character 10 was run with only two states: 0 = female foretibia without spine rows, 1 = foretibia with two or three spine rows. The ie (implicit enumeration) option resulted in 20 equally parsimonious cladograms, with a length of 28, a consistency index of 0.71 and a

retention index of 0.84. The cladogram reproduced here is representative. The cladogram and strict consensus tree were generated using the Clados program (version 1.0) of Nixon (1991). On the cladogram the black bar represents an apomorphy, the gray bar a parallelism, and the white bar a reversal.

The monophyly of *Larra* was consistently supported in the analysis by five characters (5, 7, 8, 10, 13). *Liris* appears to be paraphyletic and the attempt to resolve the relationships of this genus with the rest of the outgroup and *Larra* explains the numerous cladograms. Within *Larra* branch swapping occurred between the *bicolor* and *amplipennis* groups, and also between the *burmeisterii*, *maura* and *analís* groups. The analysis indicates a reversal of character 10 (female foretibial spine rows) in the *maura* group.

As for the outgroups, no stable set of relationships were found except for the grouping of *Liris* (*Liris*) + (*Paraliris* + *Dalara*), and no group could be reliably determined as the sister group to *Larra*. The strict consensus tree figured here shows the outgroups forming a polytomy with *Larra*.





KEY TO FEMALES OF *LARRA*

(Facial measurements should be made at 50X)

1. Pedicel densely setose (Fig. 7); outer foretibial apex not carinate (Fig. 24) ..... 2
- Pedicel asetose or nearly so, at least dorsally (Fig. 8); foretibial apex with short carina on outer face (Fig. 25) ..... 4
2. Submarginal cell II petiolate (Fig. 45) ..... *princeps* (Smith), p. 205
- Submarginal cell II not petiolate ..... 3
3. Pygidial plate broad (Fig. 37), tergum lateral to base of pygidial plate with patch of dense, subappressed setae (Fig. 38); Argentina, Bolivia ..... *stangei* Menke, p. 202
- Pygidial plate narrow (Fig. 35), tergum lateral to base of pygidial plate at most with few scattered setae (Fig. 36); widespread in South America, Central America. .... *bicolor* Fabricius, p.193 and *praedatrix* (Strand), p. 200
4. Upper interocular distance 0.51-0.56X lower interocular distance (measured tangential to upper edge of tentorial pits), gastral segments I-II red, III-V usually black; southern South America ..... *burmeisterii* (Holmberg), p. 207
- Upper interocular distance 0.32-0.50X lower interocular distance, gaster color variable ..... 5
5. From eastern North America; UID 0.43-0.50X LID .....  *analis* Fabricius, p. 210
- From Central and South America; UID 0.32-0.46X LID ..... 6
6. Pygidial plate narrow (Fig. 67); body 13-20 mm long; face with appressed silver setae between antennal socket and eye margin; thoracic pleura usually dull or weakly shiny; mandible apex often broadly rounded (Fig. 17); Mexico to Uruguay ..... *godmani* Cameron, p. 212
- Pygidial plate broad (Fig. 68); body 7-13.5 mm long; face sometimes without silver setae; thoracic pleura polished; mandible apex narrowly rounded (Fig. 16); South America. .... *altamazonica* Williams, p. 215

KEY TO MALES OF *LARRA*

(Facial measurements should be made at 50X)

1. Flagellomeres IV-V, III-V or III-VI with placoids dorsally (Figs. 13, 59-62) ..... 2
- Flagellomeres III-XI with placoids dorsally (Fig. 9) ..... 4
2. Upper interocular distance 0.51-0.57X lower interocular distance; gaster black; combined length of pedicel and flagellomere I 0.86-0.96X UID; North America .....  *analis* Fabricius, p. 210
- Upper interocular distance 0.38-0.50X lower interocular distance; gaster red, black, or mixture of both; combined length of pedicel and flagellomere I equal to or greater than UID (if not, gaster is red); neotropical ..... 3
3. Only flagellomeres IV-V with placoids (Fig. 61); mesopleuron and propodeal side polished; South America ..... *altamazonica* Williams, p. 215
- Flagellomeres III-V with placoids (Fig. 60); mesopleuron often dull; Mexico to Uruguay ..... *godmani* Cameron, p. 212
4. Submarginal cell II petiolate (Fig. 45) ..... *princeps* (Smith), p. 205
- Submarginal cell II not petiolate ..... 5
5. Labrum truncate or shallowly concave apically, not downflexed at apex (Fig. 15); volsella uniformly densely setose ventrally from base to apex (Figs. 122-123, 125-126); Argentina, Uruguay, Paraguay ..... *burmeisterii* (Holmberg), p. 207
- Labrum obtusely angular apically, the angulation downflexed (Figs. 16-18); volsellar setation variable, but always sparser or asetose between base of arms and volsellar base (Figs. 70, 74, 77, 82, 90, 110, 117) ... 6

6. Ventral surface of volsellar arm of genitalia with very long setae on apical half, abruptly changing to very short setae toward base (best appreciated in lateral view, Figs. 88-91); venter of gonostyle with scattered long setae that do not obscure surface (Fig. 84), or surface partially asetose (Figs. 96-100), or setation consisting of long fringing setae and shorter, denser setae on surface (Fig. 93). . . . . *praedatrix* (Strand), p. 200
- Ventral surface of volsellar arm either with shorter setae (Figs. 73-78), or rather densely covered with moderately long setae (Figs. 81-83, 109-110); gonostyle densely, evenly covered with long setae that obscure surface (Figs. 69, 80, 108) . . . . . 7
7. Ventral surface of volsellar arm sparsely covered with short setae that diminish in length basad (Figs. 73-78), shape of volsellar arms typically lyre-like (Figs. 70, 73, 79); widespread in South America . . . . . *bicolor* Fabricius, p. 193
- Ventral surface of volsellar arm densely covered with moderately long setae (Figs. 109-110), volsellar arms more or less straight (Fig. 109); Argentina, Bolivia . . . . . *stangei* Menke, p. 202

### BICOLOR SPECIES GROUP

*Diagnosis.*— Male flagellomeres III-XI with placoids (Fig. 9); upper interocular distance in female less than half to more than half length of lower interocular distance (UID 0.44-0.69X LID); transverse sulcus on vertex behind ocelli weakly to moderately impressed at midline; vertex of female head without deep sinus around eye margin (Fig. 3); female clypeus, frons and vertex with considerable dense setation that is often silvery (Figs. 3, 39-40), setae obscuring surface of frons at least laterally (Fig. 39-40); inner surface of female scape densely setose except for narrow asetose zone along anterior (ventral) margin (Fig. 7); female pedicel uniformly setose (punctate) dorsally, the setation less dense than that on flagellomere I (Fig. 34); surface of labrum beveled at free margin or at least sloping down there (Figs. 18, 41), free edge arcuate, angled or lobate; female mandible with long, stout, closely spaced rake setae (Figs. 18-19, 40-41); pronotum anteriorly with transversely elongate sulciform depression at midline, or with two pits (*princeps*) that are narrowly connected; lower edge of smooth, impunctate area at outer apex of foretibia not sharply carinate in female (Fig. 24); outer surface of female foretibia with row of stout, spine-like setae which often is closely paralleled anterad by row of several finer setae, and more distantly posterad by row of one to three stout setae (Fig. 22), male usually with single row of one to four finer setae; inner surface of female forebasitarsus distad of cleaning notch usually with linear asetose zone at least basally (Fig. 27) but entirely setose in one species (Fig. 26).

*Included species.*— *Larra bicolor* Fabricius, *praedatrix* (Strand), *princeps* (Smith) and *stangei* n. sp.

*Discussion.*— The numerous placoids of the male flagellum, the setose female scape and pedicel, the strong rake of the female mandible, and the beveled labrum in both sexes, characterize the *bicolor* group. Only the last two are apomorphies and neither is unique to the group. The *bicolor* group has no autapomorphies and it is the least specialized of the three New World groups. Among New World *Larra* only the monotypic *burmeisterii* group shares the male flagellar character, but female features of that group are similar to the  *analis*  group: inner surface of scape largely asetose, pedicel asetose dorsally, vertex with deep sulcus around eye, female frons largely asetose, and foretibial apex with strong carina that is about one sixth length of tibia. The female mandible of the *bicolor* and *burmeisterii* groups has a well developed rake, differing in that respect from the  *analis*  group. Although somewhat variable, females in the *bicolor* group have a more extensively and densely setose face, especially the frons, in comparison to the *burmeisterii* and  *analis*  groups. In the latter two, the frons is usually nearly asetose and polished. The gaster is always red in the *bicolor* group except in some specimens of *princeps* where it may be all black or red and black.

The Old World *amplipennis* group shares some *bicolor* group characters, but the female forebasitarsus is entirely setose within, the female scape is more broadly asetose within, and the labrum is flat to the apex, not beveled there.

The variability of the female forebasitarsus in the *bicolor* group is noteworthy. The inner surface is setose in *stangei* n. sp., similar in this respect to the *amplipennis* group. But the other members of the *bicolor* group have an asetose zone of variable length within species. The asetose zone is never as extensive as it is in the  *analis*  and *burmeisterii* groups.

Two red-abdomened females that I have studied

are problematical. One was collected at San Bernardino, Paraguay (BERLIN). It has a narrow vertex ( $UID = 0.40X LID$ ) and the inner surface of the forebasitarsus is entirely setose. This specimen is not *stangei*, the only *bicolor* group species with a setose forebasitarsus. The second female (USNM) was collected at Olinda, Pernambuco, Brasil. It displays a mixture of *bicolor* and *burmeisterii* group characters. As in the latter group the pedicel is asetose and polished, and the forebasitarsus is asetose for most of its length. In other features this specimen agrees with the *bicolor* group: the foretibia lacks an apical carina, the labrum apex slopes downward, the  $UID = 0.43X$  the  $LID$ , and the pronotum has an undivided dorsal sulcus. The San Bernardino and Olinda specimens may be freaks, or they may represent undescribed species. Only more material will resolve these problems.

The *bicolor* group contains the most commonly collected neotropical species, but after setting aside *princeps*, easily identified by its petiolate second submarginal cell, what remains is a taxonomically very difficult group, the *bicolor* complex. Before I had made a thorough study of the male genitalia, there appeared to be only one species, *bicolor*. Examination of the genitalia of "*bicolor*" males from a number of localities in South America revealed that there was considerable variation in volsellar shape and setation and also density of setation of the gonoforceps. My first thought upon realizing how variable the genitalia were in "*bicolor*" was that it was simply a very plastic species. This hypothesis was enhanced by the fact that females varied also, and I could not find characters that would divide them into two or more "species" reliably. Eventually I dissected every "*bicolor*" male available, nearly 1500 specimens. The result was the recognition of two more species, *praedatrix* and *stangei*. Except for the female of *stangei*, these three cryptic species can be separated reliably only by characteristics of the male genitalia. The females of the two most widespread species, *bicolor* and *praedatrix*, have so far proven inseparable.

In attempting to sort females of the *bicolor* complex to species, I examined the labrum, mandible, clypeus, legs, wings, thoracic sculpture, as well as the features used by Williams (1928). Among the latter are wing color, punctuation of the vertex of the head and form of the transverse depressions behind the ocelli, proportions of basal flagellomeres, comparisons of flagellomere lengths and distance between the eyes at the vertex,

propodeal sculpture including presence or absence of a median carina, and shape of the pygidial plate. Under scrutiny none of these permitted recognition of more than one taxon. The labrum seems highly plastic. Female wing color varies geographically in the *bicolor* complex; they may be pale basally, or entirely infumate. The degree of punctuation of the vertex varies in females from widely scattered pin prick punctures with a few larger punctures sometimes mixed in, to dense, large punctures separated by less than a puncture diameter. The shape of the vertex depressions noted by Williams vary and thus are not useful to separate species. Various head measurements, often diagnostic in wasps, offered no help in the *bicolor* complex. For example, the upper interocular distance varies within these species from less than half to three-fifths the length of the lower interocular distance. The proportions of the basal flagellomeres also vary. The median longitudinal carina of the propodeal dorsum varies from present to absent within species, and propodeal sculpture is variable. The shape of the female pygidial plate is somewhat variable, and the only species in which it appears to be useful at the species level is *stangei*.

Before reaching the conclusion that females of *bicolor* and *praedatrix* were truly inseparable, I examined material that was collected at the same location and date as known males of these species. If females of both species were present, I can only conclude that they are unrecognizable. I had a large sample of *bicolor* complex material from Saavedra, Bolivia in which males of *bicolor* and *praedatrix* were nearly equally numerous, 343 and 304 specimens, respectively. There were 500 females, but I could not separate them into two species. I also studied laboratory reared material from Saavedra sent by Fred Bennett, University of Florida, Gainesville, Florida. He had F1 and sometimes F2 offspring from females and all material was correlated by numbers. Male progeny from the mothers offered positive means of associating males and females of *bicolor* and *praedatrix*. I had hoped that this material would permit detection of characters for separating females of these two species, but such was not the case. All but one of the 14 females proved to be *bicolor* based on male offspring, and the 13 specimens of *bicolor* amply demonstrated how variable the head punctuation and other characters are in that species. Features of the single female of *praedatrix* fell within the variation of *bicolor*.

*Larra bicolor* and *praedatrix* are largely sympatric in South America and often occur together. The genitalia of *bicolor* vary a little over the range of the species, but variation in *praedatrix* is bewildering (see Figs. 84-107). Further study of *praedatrix* may indicate that it is a complex of cryptic species, but laboratory rearing of material and sophisticated techniques like cuticular hydrocarbon studies may be required to resolve this.

Finally, I have 39 males, all from Venezuela, whose genitalia are fairly similar to *stangei*, a new species from southern Bolivia and northwestern Argentina whose female is fairly reliably separable from *bicolor* and *praedatrix* by the form of the pygidial plate and associated setation. Presumptive females of the Venezuelan taxon are, however, inseparable from those of *bicolor* / *praedatrix*, and it may be that the male genitalia simply represent an extreme variant of *bicolor*. This is another problem for future study.

The absence of female differences poses a critical nomenclatorial problem: the lectotype of *bicolor*, the oldest name, is a female. I have arbitrarily interpreted *bicolor* as the species that was introduced to Puerto Rico and later Florida. The treatment of younger names based on females has also been problematical, and these are discussed under *bicolor* and *praedatrix*.

The species treatments that follow, with the exception of *princeps*, are based largely on male characters because of the female problems discussed above. A composite female description for *bicolor* / *praedatrix* is presented under the *bicolor* treatment that follows.

### ***Larra bicolor* Fabricius**

Figs. 1, 3, 7, 9-12, 18, 22, 24, 27, 29-36, 39, 69-79

*Larra bicolor* Fabricius, 1804:221. Lectotype female: "America meridionali" (COPENHAGEN), designated by van der Vecht (1961:17).

*Tachytes pagana* Dahlbom, 1843:132. Holotype male: "insula St. Croici" (= St. Croix, Virgin Is.) (BERLIN). Synonymy by Patton (1881:389). Type examined by Stadelmann (1897:255).

*Larrada americana* Saussure, 1867:74. Lectotype male: Caracas, Venezuela (GENEVA), present designation. Synonymy by Patton (1881:389); van der Vecht (1961:17).

*Larrada gastrica* Taschenberg, 1870:5. Lectotype male: "Paraná", [Brasil or Argentina] (HALLE), designated by Menke (in Bohart and Menke, 1976:238). NEW SYNONYM.

*Larra guiana* Cameron, 1912:433. Holotype female: Guyana (BMNH). NEW SYNONYM.

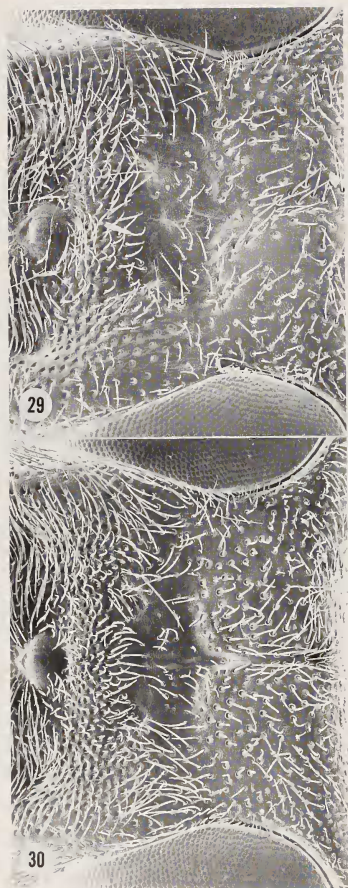
*Larra scaptesiccia* Williams, 1928:58. Holotype female: Belém, Brasil (BISHOP). NEW SYNONYM.

**Male description.**— (951 specimens of which 343 are from Saavedra, Bolivia). Male identifiable only by genitalia: ventral surface of gonoforceps densely covered with uniformly long setae that obscure surface (Fig. 69); ventral surface of volsellar arms sparsely setose, in lateral profile all setae are fairly short although those at apex are longest and there is a gradual shortening of the setae basad (Figs. 75, 78), toward the base of the of the volsellar lobe the setae are restricted to outer area (Figs. 70, 73, 76, 79); in ventral view margins of volsellar arm broadly sinuate, the apex usually acuminate and curving away laterad (Figs. 70, 73, 79); outline of apicodorsal crest of volsellar arm highly variable in lateral profile.

UID0.54-0.73X LID; vertex behind ocelli variably covered by large punctures (Figs. 29-30) that are crowded (separated by a puncture diameter or less), or more widely spaced (separated by 2-4X a puncture diameter, usually unevenly so); transverse impression behind ocelli variable, often forming an angle at midline, the angle often terminating in a pit, sometimes with median sulcus or impression beyond angle that may reach rear edge of vertex; labrum usually arcuate, but free edge occasionally straight, surface of labrum usually impunctate as it slopes down to setose free edge, occasionally slope is punctate. Propodeal dorsum usually with median, longitudinal carina on basal one third or fourth, occasionally extending to apex, sometimes nearly absent. Forewing from base to level of stigma paler (clear to yellowish) than infusate apex; submarginal cell II variable in shape, but very rarely petiolate on marginal cell. Gaster red; tergum VII with or without lateral angle or carina delimiting a pygidial plate; sternum VIII variable, apex notched or rounded. Length 8-14 mm.

**Discussion.**— The volsella nearly always identifies males of *bicolor*. The somewhat lyre-like form of the two volsellar lobes with their attenuate apices and rather sparse, short setation ventrally are unique. Occasionally the lobes are atypically narrow (Figs. 76, 79), and sometimes the apices are somewhat blunt and not divergent (Fig. 76), but the sparse, short setation is still distinctive. To really appreciate the shortness of the volsellar lobe setation the structure should be viewed in lateral profile (Figs. 75, 78). In the sibling species *praedatrix* the volsellar lobes vary in shape and sometimes resemble those of *bicolor*, but the setae on the apical half are very long and abruptly change to very short setae beyond that point (Figs. 89-91). In *bicolor* the





Figs. 29-30. Vertex of male head of *bicolor* from Puerto Rico showing variation in punctation.

setae gradually shorten from apex to base. Furthermore, the gonostyle in *praedatrix* is never covered densely by the uniformly long setae found in *bicolor*. In *stangei* the volsellar lobes are straight and densely covered ventrally by long setae (Figs. 109-110).

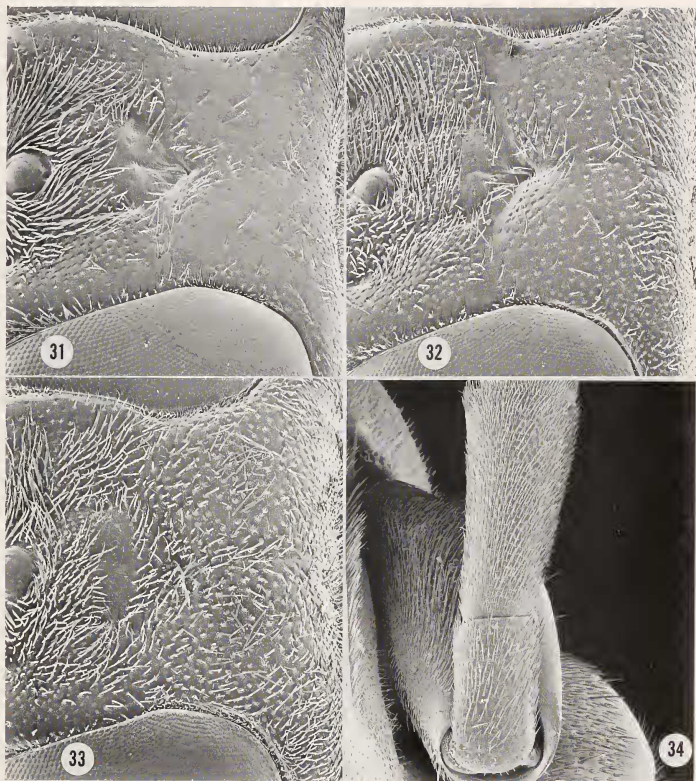
I have 39 males (MARACAY, USNM, FSDA, CORNELL) from several localities in Venezuela (Map 4) whose status is unresolved. The volsellar setation is similar to that of *stangei* (Figs. 81-83), but the lobes are lyre-like as in *bicolor* (Fig. 81), and the gonostyle setation is like *bicolor* (Fig. 80). Putative females of these Venezuelan specimens are not *stangei*. Thus the Venezuelan males may represent a new species, or an extreme variant of *bicolor*. The latter hypothesis is supported by 12 males that I collected in 1985 at Hato Masaguaral south of Calabozo, Venezuela (USNM). Three are typical *bicolor*, ten represent the unresolved taxon, and one has volsellar setation that is somewhat intermediate.

Variation in the upper interocular distance is fairly random geographically, but the shortest UID's occur in the smallest specimens. Likewise, the density of vertex punctation, development of the propodeal carina, etc. are also random. The shape of forewing submarginal cells varies and occasionally the inner and outer veinlets of II meet on the marginal cell. In one male from Paraguay (CSDA) these two veinlets form a very short petiole before reaching the marginal cell.

*Female description*.—(1158 specimens of which 500 are from Saavedra, Bolivia).

The following descriptive notes apply to females of *bicolor* and *praedatrix* since they are indistinguishable.

UID 0.46-0.63X LID; transverse impression behind ocelli usually deeply, obtusely angular, but occasionally weakly impressed or absent, in the latter a small circular fossa remains where apex of angle would be; vertex punctation varies from very sparse pin prick punctures with scattered larger punctures to very dense macropunctation (Figs. 31-33); labrum typically flat with deflexed thickened apex (Fig. 18) that varies from impunctate or punctate, sometimes with prominent corners in the latter, outline of free margin highly variable; pronotum with transversely elongate sulciform depression anteromedially (also present in male); propodeal dorsum with median carina of varying length, or carina absent; forewing bicolor (clear basad of stigma) or uniformly infuscate; submarginal cells II and III variable in shape; gaster

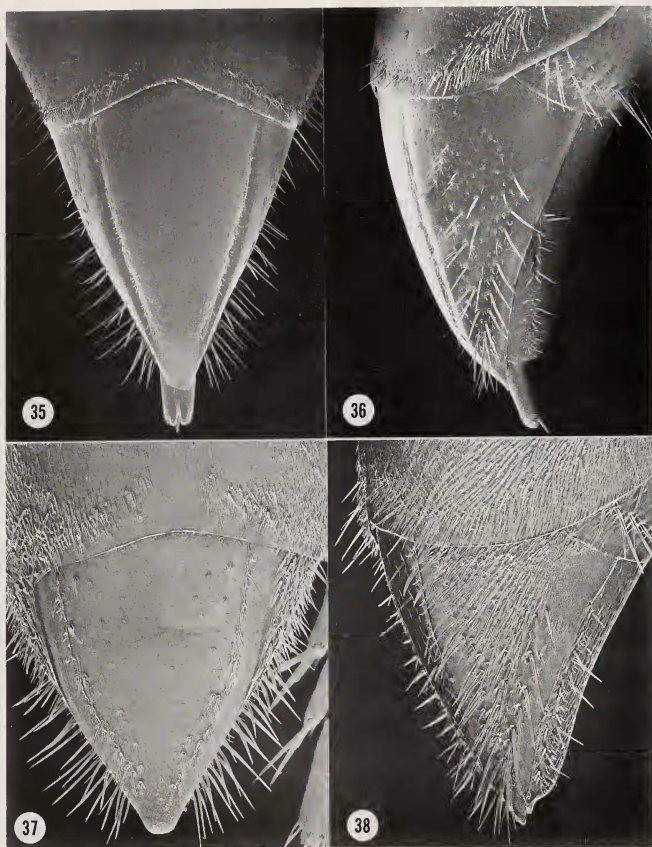


Figs. 31-34. Female head features of *bicolor*. 31-33, Vertex showing punctation behind ocellar triangle. 31, Specimen from Puerto Rico. 32, Specimen from Campinas, Brasil. 33, Specimen from Entre Rios, Argentina. 34, Dorsal surface of pedicel and flagellomere I.

red except pygidial area blackish in occasional specimens from Argentina; pygidial plate typically narrow, weakly convex (Fig. 35), but rarely broader and nearly like *stangei*; tergum lateral to pygidial plate typically only with scattered, long, erect setae that usually become sparser toward base (Fig. 36), occasionally, however, some shorter, subappressed setae are clustered near base as in *stangei* (some

material from Paraguay). Length: 9.5-20 mm.

*Discussion of female variation.*— Some variation is geographic. Bicolored wings are typically found only in females from Mexico; El Salvador; parts of Colombia, Peru, Venezuela, and French Guiana; the lower Amazon drainage (east of Santarém in Pará); Puerto Rico; and Florida. Dark wings predominate south of the Amazon Basin, but



Figs. 35-38. Sixth gastral segment of female *Larra*. 35-36, *L. bicolor*. 35, Pygidial plate. 36, Lateral view of right side showing setation. 37-38, *L. stangei*. 37, Pygidial plate. 38, Lateral view of right side showing setation.

material from Guatemala, Costa Rica, Trinidad, the Guianas, and parts of Colombia, Peru and Venezuela usually have evenly infumate wings. The type and density of punctation on the vertex more or less coincides with wing color. Most female

wasps with evenly infumate forewings have dense macropunctuation on the vertex. Exceptions to this rule occur in Venezuela, Trinidad, the Guianas, Peru, Mato Grosso in Brasil, Paraguay and Argentina where the vertex may have sparse pin





prick punctation with scattered larger punctures in dark-winged females. Punctuation intergrades occur everywhere of course. Occasional specimens have a broad pygidial plate or have a cluster of shorter, subappressed setae lateral to it basally, as in *stangei*, but I have not seen specimens with both conditions.

*Distribution based on males* (Map 1) and *females* (Map 2).—Widespread in South America: Colombia to about the 38th parallel in Argentina. Also Trinidad, Puerto Rico (introduced) and Florida (introduced). I have seen no males of *bicolor* from Central America, so all the female records from there (Map 2) may pertain to *praedatrix*.

*Florida material*.—*Larra bicolor* was first liberated at Gainesville, Tampa, and Fort Lauderdale, Florida in 1981 (Hudson et al., 1988). The following year additional releases were made at Bradenton and Lakeland, but the species only became established at Fort Lauderdale. The introduced wasps were collected around Isabella, Puerto Rico. In 1988-1989 Bolivian material of "*bicolor*" from Saavedra was liberated at sites in Alachua County, Florida (Bennett et al., 1990), but according to Fred Bennett (personal communication) the wasps apparently did not become established.

Floridian females have the sparse pin prick punctation on the vertex typical of Puerto Rican material, the latter the offspring of wasps collected originally around Belém, Brasil (Wolcott, 1941). The Fort Lauderdale population has not spread much according to Fred Bennett. I have studied a single female collected at Watson's Hammock, Big Pine Key in Monroe Co., Florida on August 28, 1986 by S. & J. Peck (ALBERTA). This female is puzzling because it has moderately dense punctation on the vertex, and the punctures are intermediate between pin pricks and macropunctuation similar to material from Mexico and parts of Central America. It has bicolored wings just like the Fort Lauderdale material, but the denser head punctation suggests that this female is not offspring from the Fort Lauderdale population. Possibly it represents a chance introduction from Central America or an undetected native population. Positive identification of the Big Pine Key female as *bicolor* will have to await capture of males.

*Type notes*.—I have not examined the lectotype of *L. bicolor* designated by van der Vecht (1961), but I have studied the material that he compared with it (USNM, LEIDEN). From van der Vecht's (1961) notes and the appearance of his homotypes, it is clear that the lectotype has bicolored forewings ("with faint yellow tinge . . . outer half slightly

darker"). The vertex of the head posterior to the ocelli is very sparsely covered with a mixture of pin prick and regular punctures, the latter far fewer in number. The propodeum has a median longitudinal carina on basal half, and the tegula is amber colored. I am arbitrarily interpreting Fabricius' type as conspecific with the male that I call *bicolor*.

I have examined a male specimen bearing a handwritten label "*Larrada pagana* Dahlb.". The label does not closely resemble the two examples of Dahlbom's handwriting illustrated by Horn and Kahle (1937), but it is similar to the example of Stadelmann's writing in the same work. The locality label on the pin says "Brasilien" which disagrees with Dahlbom's stated origin for the specimen ("ex insula St Crucis dedit Amic. Sommer in Altona mense Julio 1838"). Thus there is doubt about this specimen being the type of *pagana*. On the other hand, *Larra* apparently did not occur in the West Indies until *bicolor* was introduced to Puerto Rico by Wolcott in 1936 (see Wolcott 1936), and I have seen no material from St. Croix or any other Caribbean island except Trinidad. Thus Dahlbom either gave erroneous locality information or his type specimen was mislabeled. In any event, the genitalia of the presumed type of *pagana* are typical for *bicolor*, and I regard Stadelmann's (1897) synonymy as correct.

Saussure's *Larrada americana* was described from three females and a male from Caracas, Venezuela, and a female from "Brasilia". He had an additional female from "Cayenna" that he tentatively treated as a "var.". I have examined the Caracas material, all housed at the museum in Geneva, and the male is a typical *bicolor*; I have labeled it as lectotype. Its genitalia fall within the limits of *bicolor*. The other specimens have not been located.

Taschenberg (1870) described *gastrica* from two males and three females that were taken at three different localities: Paraná, Panda oriental (an area in Minas Gerais, Brasil), and Venezuela. I designated (Menke 1976:238) a male from Paraná as lectotype. I presume that Paraná refers to the state in Brasil, but there is also a city, Paraná, in Entre Rios, Argentina. The genitalia of the lectotype fall within the limits of *bicolor*.

The holotype of *Larra guiana* Cameron is a female with uniformly infumate forewings. The vertex of the head is sparsely covered with a mixture of pin prick and regular punctures, the tegula is amber colored on its posterior half, and the propodeal dorsum has a median carina on its basal third. Cameron's label reads "*Larra guyana* Cameron, Brit.





Guyana", but the name is spelled *guiana* in the original description. Synonymy of *guiana* with *bicolor* is presumptive because the type is a female.

The holotype of *sapteriscica* Williams appears to be only a small example (11.3 mm. long) of *bicolor*, but it could also be *praedatrix*. The vertex punctuation is similar to that described for the types of *bicolor* and *guiana*. But there is no trace of a carina on the propodeal dorsum of the type, or in five of the six topotypical female paratypes, but one of the latter has a long carina. The genitalia of the two topotypical male paratypes are missing unfortunately. Williams' (1928) description and figure suggest that they were not of the typical *bicolor* type.

### **Larra praedatrix (Strand)**

Figs. 84-107

*Notogonia praedatrix* Strand, 1910:159. Holotype male: Calle S. Miguel, in Asuncion, Paraguay (BERLIN). NEW COMBINATION.

*Larra paraguayana* Strand, 1910:158. Holotype female: Calle San Miguel in Asuncion, Paraguay (BERLIN). NEW SYNONYM.

*Notogonia gastrifera* Strand, 1910:160. Lectotype male: Villa Morra, [Asuncion], Paraguay (BERLIN), present designation. NEW SYNONYM, new combination.

*Larra pacifica* Williams, 1928:55. Holotype female: Bucay, Ecuador (BISHOP). Provisional NEW SYNONYM.

**Male description.**—(479 specimens, of which 304 are from Saavedra, Bolivia). Male identifiable only by genitalia. Typical form as follows: ventral surface of gonostyle with widely spaced, long setae of variable length, those along the margins longer than most of those on the ventral surface, and increasing in length toward base (Figs. 84-85); ventral surface of volsellar arms sparsely setose, in lateral profile those on apical half very long, abruptly changing to very short setae basad (Figs. 88-91); in ventral view outer margins of volsellar arms straight, the arms converging (Fig. 85).

Variations from this typical form are many (Figs. 92-107), but most share one diagnostic feature, the very long setae on the apical half of the volsellar arm that abruptly change to very short setae beyond; in a few males, however, the long volsellar setae continue all the way to the base of the arm or nearly so (Figs. 92-95).

Sometimes the volsellar arms are much narrowed and straight (Figs. 100-101), or as in *bicolor* they may curve outward somewhat at the apex, but the latter is usually rounded (Fig. 107). The lateral

profile of the volsellar arm crest varies considerably (Figs. 89, 102, 104, 106), and the apex may be sharp (Figs. 88, 94) or rounded (Fig. 107). Most genitalic variants involve gonostyle setation. Sometimes the gonostyle has a narrow asetose zone along the inner margin (Fig. 96). This is often accompanied by an increase in the overall density of setation with setae along the center of the gonostyle being uniformly shorter, sometimes considerably shorter, than those along the margins (Fig. 97). Sometimes the asetose area includes most of the ventral surface of the gonostyle (Figs. 98-100).

UID 0.52-0.73X LID; vertex similar to *bicolor*; labrum usually arcuate but free edge sometimes lobe-like, surface of labrum impunctate as it slopes down to setose free edge, occasionally slope is punctate. Propodeal dorsum without or with median longitudinal carina of variable length. Forewing paler between base and stigma than infusate apex; submarginal cell II not petiolate. Gaster red; tergum VII with or without lateral angle or carina delimiting pygidial plate; sternum VIII variable, apex notched or rounded. Length 7.5-15 mm.

**Discussion.**— Although there is considerable plasticity in the male genitalia, the volsellar arm setation is usually diagnostic: the setae on the apical half are very long, abruptly changing to very short setae beyond (Figs. 89-91). In some specimens the long setae continue to the base of the arm or nearly so, but they are always restricted to the inner margin of each arm (Fig. 94). Such specimens occur in Costa Rica, and the Brazilian states of Pará, Bahia and Espírito Santo. Occasional specimens of *bicolor* and *stangei* with similar volsellar arm setation have been mentioned under those species treatments, but they have uniformly long, dense setation on the venter of the gonostyle. The occasional males of *praedatrix* with long setae nearly to the volsellar arm base have sparser gonostyle setation characteristic of this species.

Specimens with a narrow asetose zone on the gonostyle (Figs. 96-97) occur in Guatemala, El Salvador, Costa Rica, Colombia, Ecuador, and Argentina. Largely asetose gonostyles (Figs. 98-100) have been noted on specimens from Guatemala, Costa Rica, Bolivia, Mato Grosso and Ceará in Brazil, Paraguay, and Argentina. The great variation in gonostyle setation (Figs. 84, 93, 96-100) is perplexing and there is no correlation with variation in volsellar form and setation. The various volsellar types described and illustrated here occur with most of



the different gonostyles, not just those shown in the SEM figures. There are so many intermediates that I have been unable to identify more than one species. Nevertheless, future work may indicate that *praedatrix* consists of several sibling species. On the other hand, it is still possible that *praedatrix* may prove to be conspecific with *bicolor*. If so, the latter would be an unusually plastic species in terms of male genitalia.

*Female*.—Indistinguishable from *bicolor*. See that species for particulars.

*Distribution based on males* (Map 3).—Known from the state of Vera Cruz in Mexico to Buenos Aires Province in Argentina, but apparently mostly absent from the Amazon Basin. *Larra praedatrix* is largely sympatric with *bicolor* in southern South America, but seems to replace the latter species in Central America and the lower slopes of the northern Andes.

*Type notes*.—Bohart and Menke (1976) incorrectly listed *praedatrix* under the genus *Liris*. Strand's (1910) holotype is a *Larra*, and was probably collected with the females of *paraguayana*; all have similar locality labels. The male genitalia of the holotype of *praedatrix* are identical to figures 84-87.

Strand (1910) tentatively identified two female specimens from Paraguay as *Larra rubricata* Smith, a red abdomened species now placed in the genus *Liris*; he also provisionally named these specimens as "*L. paraguayana*" in the event that they should prove to be distinct from *rubricata*. Strand indicated that the larger specimen was the "Type". The holotype was collected June 10, 1906. I have examined both females and am assuming that the holotype is conspecific with the holotype of *praedatrix*. As first revisor, I have selected *praedatrix* for the name of this species because it is based on a male.

*Notogonia gastrifera* Strand was described from three males all from the same locality. I have selected and labeled one as lectotype. Its genitalia are of the typical *praedatrix* type. It was collected Nov. 9, 1905; the other two were collected Jan. 3, 1906. Bohart and Menke (1976) incorrectly listed *gastrifera* under the genus *Liris*.

The holotype of *Larra pacifica* Williams is a female from Bucay, Ecuador. His paratypes, all males from Tena, Ecuador, are *praedatrix*. Since I have no authentic males of *bicolor* from Ecuador, but quite a few of *praedatrix*, I am tentatively synonymizing *pacifica* with *praedatrix*.

## *Larra stangei* Menke, new species

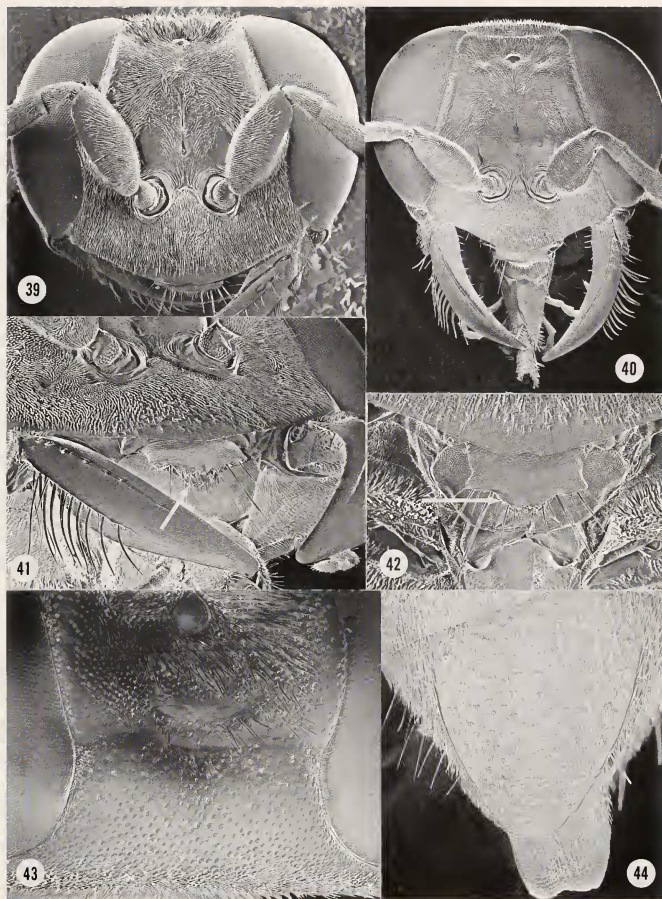
Figs. 19, 26, 37-38, 40-44, 108-111

*Description of male*.—(11 specimens). Separable from other members of the *bicolor* complex only by genitalia (Figs. 108-111): ventral surface of gonostyle densely covered with uniformly long setae that obscure surface (Fig. 108); ventral surface of volsellar arms densely, uniformly covered with long setae (Fig. 109); in ventral view, outer margin of volsellar arm straight (Fig. 109); apicodorsal crest of volsellar arm not or only slightly incurved in dorsal view.

UID 0.63-0.69X LID. Vertex behind ocelli with transverse impression that does not form an obtuse angle at midline, macropunctate, punctures nearly contiguous. Labrum impunctate, surface smoothly sloping down to free margin. Median longitudinal carina of propodeal dorsum sometimes absent, but usually extending to apex. Wings uniformly infumate in Argentine specimens, forewing bicolor and hindwing largely pale in Bolivian material; second submarginal cell of forewing not petiolate. Gaster red; tergum VII with broad, flat pygidial plate delimited by sharp lateral carinae (Fig. 44); sternum VIII with shallow apical V-notch (Fig. 44). Length 11-14 mm.

*Female*.—(17 specimens). UID 0.53-0.57X LID; transverse impression behind hindocelli obtusely angular, vertex densely bipunctate, macropunctures much more numerous (Figs. 43); surface of labrum flat, sharply truncate apically, free edge thickened and forming prominent deflexed lobe (Figs. 41-42); pronotum anteriorly with transversely elongate sulciform depression at midline (also present in male); inner surface of forebasitarsus without asetose zone distad of cleaning notch (Fig. 26); propodeal dorsum with or without median, longitudinal carina; gaster red, tergum VI with broad pygidial plate that is flat on apical half, and whose margins are cariniform on apical half (Fig. 37), surface of tergum lateral to plate apex with many long, stiff setae that become shorter, denser and more appressed toward base (Figs. 37-38); wings uniformly infumate in Argentine specimens, forewing bicolor and hindwing largely pale in Bolivian specimens. Length 13.5-18.5 mm.

*Discussion*.—The densely setose volsella is the most diagnostic male feature of *stangei* although some male *Larra* from Venezuela have similar genitalia. In the Venezuelan material, however, the volsellar lobes curve outward apically in ventral



Figs. 39-44. Features of *bicolor* group. 39-40, Female face. 39, *bicolor*. 40, *stangei*. 41-42, Labrum and associated structures in female of *stangei*. 41, Oblique view of mandible and labrum (arrow points to deflexed apical lobe of labrum). 42, Closeup of labrum. 43, Female vertex of *stangei* showing ocelli and postocellar punctation. 44, Male tergum VII showing pygidial carinae, apex of sternum VIII visible below.





*Smithophanes*. Smithophanes 1983  
Prepared by Theophilus Boris Greenwald

view (Fig. 81), just as in *bicolor*, and these specimens may be variants of that species and not *stangei* (see *bicolor* treatment). The broad, flat female pygidial plate of *stangei* is distinctive in this sex (Fig. 37), but by itself is unreliable because of variation in this structure in *bicolor/praedatrix*. Usually, however, the latter do not have short, dense, subappressed setae on the side of the tergum (Fig. 38), or if they do, the plate is narrow. In older, worn female specimens of *stangei* the subappressed setae may be abraded, but their pits are still visible. The absence of a clearly demarked asetose zone on the forebasitarsus (Fig. 26) is another apparent character of females of *stangei*, but in view of the variation in the development of this zone in the other species of the group, and the small sample size for *stangei*, the reliability of this character is unknown.

Two males from Rosario de Lerma, Salta, Argentina (CSDA, FRITZ) have puzzling genitalia. In one the volsella has long setae along the inner part of each arm from apex to base, but they are not as dense as in *stangei*, and laterally the setae are shorter. The apicodorsal crest of the volsellar arm is somewhat higher than the average condition in *stangei*, and it curls inward strongly in dorsal view. In the other specimen the volsellar setation is typical of *stangei* but the volsellar arm is constricted subapically and the apicodorsal crest is sinuate and incurved. In view of the genitalic variation in other species, these two specimens probably are *stangei*, but I have not included them among the paratypes. Curiously a third male collected at the same place is a typical *bicolor* (CSDA).

**Etymology.**— I take pleasure in naming this wasp after my long time friend, Lionel Stange, who collected nearly half of the known material.

**Distribution** (Map 4).— Northwestern Argentina, southern Bolivia.

**Types.**— **Holotype male:** BOLIVIA, Santa Cruz: Sand dunes at El Palmar Oratorio, about 40 kms southeast of Santa Cruz, Jan. 25, 1980, Lionel A. Stange (FSDA). **Paratypes:** BOLIVIA, Santa Cruz: same data as holotype, 5 males, 4 females, L. A. Stange (FSDA, USNM); Santa Cruz, one male, Feb. 10, 1971, M. Fritz (FRITZ). ARGENTINA, Salta: Alemania, one male, five females, Feb./Mar. 1983, M. Fritz (FRITZ); La Viña, one male, three females, Dec., Feb. 1983-1984, M. Fritz, M. Wasbauer (FRITZ, CSDA); Tartagal, two males, three females, Nov. 1971, M. Fritz (FRITZ); Guachipas, one female, Feb. 1989 (FRITZ); Coronel Moldes, one female, Feb. 1990 (FRITZ).

## **Larra princeps (Smith)**

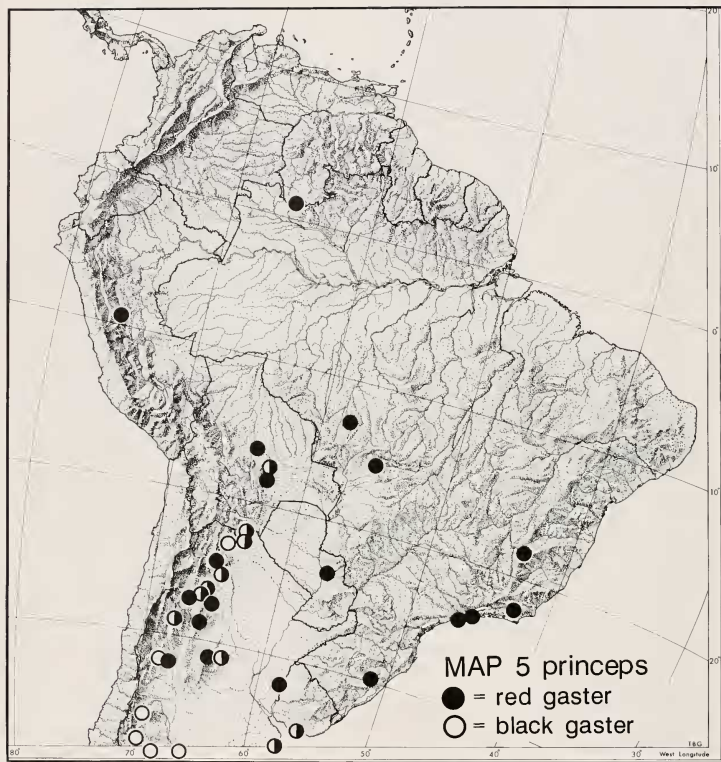
Figs. 45-46, 112-119

*Larraxena princeps* Smith, 1851:30. Lectotype female: "Brazil" (BMNH), present designation.

**Description.**— (126 males, 124 females): Male UID 0.50-0.62X LID; female UID 0.44-0.50X LID (as measured tangential to upper edge of antennal sockets). Male vertex behind ocelli with transverse impression that is usually deeply, triangularly depressed at middle; deep groove often extending posterad from apex of this depression; macropunctate, punctures nearly contiguous to one diameter apart. Female vertex similar except no groove extending posterad from triangular depression and punctures varying from fine to coarse and often separated by 2 or 3 puncture diameters. Labrum impunctate in both sexes, surface smoothly sloping down to free margin that has a few marginal punctures. Pronotum anteriorly with pair of oval pits that are usually narrowly connected. Propodeal dorsum carina usually extending nearly to apex, but sometimes much shorter or even absent. Wings evenly infumate with rare exceptions; second submarginal cell petiolate on the marginal cell (Fig. 45), petiole rarely very short or absent (Fig. 46). Gaster black or red, sometimes red with black areas at tergal and sternal margins; female tergum VI and pygidial plates same as *bicolor*; male tergum VII without pygidial carinae; male sternum VIII variably emarginate apically; ventral surface of gonostyle uniformly covered with dense, long setae that obscure surface (Fig. 112); volsellar arms broad, densely covered with long setae ventrally that obscure surface (Figs. 112, 116-117); apicodorsal crest of volsellar arm not incurved in dorsal view (Fig. 118). Males 9-16 mm long, females 13-20 mm. long.

**Discussion.**— The petiolate second submarginal cell immediately identifies *princeps*. I have seen two Argentine females in which the cell is not petiolate on one wing (Fig. 46), so it is likely that rare individuals might have non-petiolate cells in both wings. Separation of them from *bicolor/praedatrix* should be possible by the presence of two pronotal pits. The male genitalia of *princeps* are fairly uniform and quite distinctive, particularly the broad volsellar arms that are densely covered with setae (Figs. 116-117).

*Larra princeps* is the only species in the *bicolor* group that has two color forms. All black specimens



occur mainly in the southern part of the species' range, but both color morphs occur together especially along the eastern side of the Andes in Argentina (Map 5). Red morphs predominate, however. Exceptions to the darkly infumate wings occur in Peru and Entre Rios Prov. in Argentina where the wings are paler toward the base and the infumation is less dense.

*Distribution* (Map 5).— *Larra princeps* is a commonly collected species in Argentina, but the species appears to have a fairly wide distribution in South America based on a few scattered records in Peru, Venezuela and Brasil.

*Type notes*.— I have examined the two female syntypes described by Smith in 1851. Both have a red abdomen and typical wing venation. I have

placed my lectotype label on the specimen that already had a circular "type" label.

#### BURMEISTERII SPECIES GROUP

**Diagnosis.**— Male flagellomeres III–XI with placoids; upper interocular distance in female at least half length of lower interocular distance; transverse sulcus on vertex behind ocelli weakly to moderately impressed at midline; vertex of female head usually with narrow, deep sinus around eye (Fig. 49); female frons beneath transverse swelling polished, nearly impunctate and largely asetose except at level of antennal sockets, clypeus laterally, and vertex (Fig. 47); inner side of female scape largely asetose, with only few scattered setae basally (Fig. 48); female pedicel asetose dorsally and ventrally, polished, at most with a few scattered setigerous punctures (Fig. 48); labrum flat, at most narrowly downflexed at midapex (Fig. 15); female mandible with numerous long, stout rake setae (Fig. 15); pronotum anteriorly with pair of oval pits at midline; lower edge of smooth, impunctate area at outer apex of female foretibia margined by sharp carina that extends about one sixth tibial length (Fig. 51), male with much shorter carina; outer surface of female foretibia with row of stout, spine-like setae that often is closely paralleled anterad by row of several finer setae, and more distantly posterad by row of one or two stout setae (Fig. 50), male usually with single row of one or two fine setae; inner surface of female forebasitarsus distad of cleaning notch with asetose linear zone that extends to apex (Fig. 52).

**Included species.**—*Larra burmeisterii* (Holmberg).

**Discussion.**— This group displays a curious mixture of characters. The male has a plesiomorphic antenna just like the *bicolor* group. The female, however, shares several apomorphic features with the  *analis*  group (asetose pedicel, asetose inner surface of scape, frons largely asetose and polished, sinus present around upper margin of eye, and carinate foretibial apex). The ocular sinus is not as pronounced as in the  *analis*  group and it represents an intermediate condition. The upper interocular distance in the female of  *burmeisterii*  is broader than in the  *analis*  group.

Apomorphies of the  *burmeisterii*  group include the shiny, asetose female pedicel, the female ocular sinus, the shiny asetose and nearly impunctate female frons, the moderately well developed female mandibular rake setae, the pair of pronotal pits, the

foretibial carina in both sexes, and the asetose linear area on the inside of the female forebasitarsus. None are unique to the group.

The female pedicel of the Old World species  *anathema*  (Rossi), the type species of  *Larra* , approaches the condition found in  *burmeisterii* . It is polished dorsally but the surface is sparsely setose, and the outer and ventral surfaces are densely setose. The inner surface of the female scape of  *anathema*  is polished and largely asetose just as in  *burmeisterii* . The female of  *anathema*  lacks a deep sinus around the upper margin of the eye, the foretibial carina is absent, and the forebasitarsus has only a vaguely defined asetose area basally. Both sexes of  *anathema*  have a flat labrum just like  *burmeisterii* , however. The Australian  *L. melanocnemis*  Turner, which probably belongs in the  *anathema*  group, shares most of the latter's features but the female forebasitarsus has a distinct asetose zone.

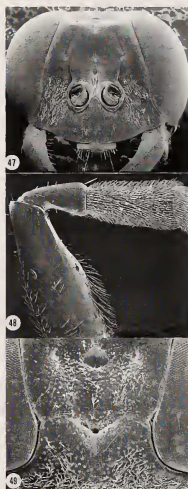
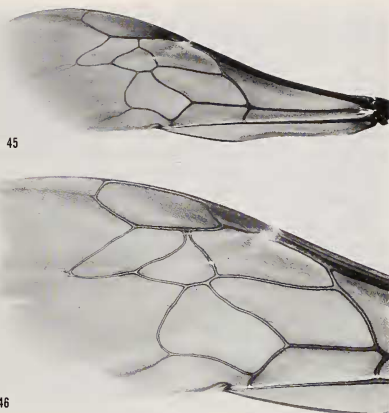
The gaster in  *burmeisterii*  may be red, black or combinations of both colors.

#### *Larra burmeisterii* (Holmberg)

Figs. 15, 47–52, 120–127

*Larrada burmeisterii* Holmberg, 1884:221. Holotype female: Colonia, Paraguay (destroyed).

**Description.**— (72 males, 183 females): Male UID 0.60–0.66X LID; female UID 0.51–0.56X LID (as measured tangential to upper margin of tentorial pits). Male vertex behind ocelli with weakly to strongly impressed angular depression at midline posterior to which is a narrow, linear impunctate zone; macropunctate, punctures about a diameter apart or less. Female vertex with strong angular depression behind ocelli, and sometimes with narrow, linear impunctate zone posterior to it, this area often somewhat elevated even if punctate; punctures nearly contiguous posteriorly but becoming sparser toward transverse impression, sometimes impunctate and polished next to it (Fig. 49). Labrum scarcely projecting beyond clypeus, especially in male, polished, impunctate, flat to free margin although sometimes indented there at midline, apex slightly arcuate, truncate or shallowing emarginate (Figs. 15, 47). Propodeal dorsum carina present and of variable length, or more frequently absent. Wings darkly infumate in female, clear or weakly infumate in male; second submarginal cell of forewing not petiolate. Male



Figs. 45-46. Left female forewing of *Larra princeps*. 45, Wing with normal petiolate second submarginal cell. 46, Wing with aberrant second submarginal cell (right wing is normal).

Figs. 47-49. *Larra burmeisterii*, features of female head. 47, Face. 48, Inner side of scape, pedicel and flagellomere I of left antenna. 49, Vertex.

abdomen all red or all black, but sometimes first two or three segments are red, the remainder black; female abdomen sometimes all red, but usually segments I-II and VI red, III-V black, or occasionally segments I-III red, remainder black; female tergum VI and pygidial plate similar to that of *bicolor*; male tergum VII usually with pygidial carinae, sternum VIII usually notched apically but sometimes entire; ventral surface of gonostyle densely covered with long setae that obscure surface (Fig. 120), volsellar arm of uniform width to rounded apex (Fig. 124), or constricted subapically (Fig. 121), entire venter of volsellus densely covered with long setae (Figs. 121-126); apicodorsal crest of volsellar arm variable in lateral profile (Figs. 123, 126). Males 8.5-13.5 mm long, females 11-18.5 mm long.

*Discussion.*—The male of *burmeisterii* is reliably identified only by genitalic characters, primarily the completely setose volsella (Figs. 122-123, 125-126). The flat, non-beveled labrum is useful, but often the labrum is concealed in dead material. The female can be identified by the polished, nearly

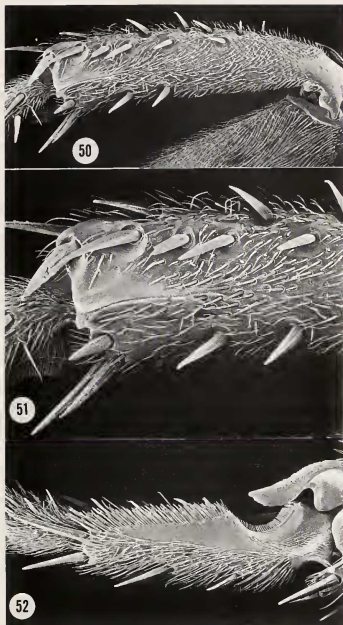
asetose pedicel and the broad upper interocular distance (equal to at least half the lower interocular distance). Color is also useful. No other species within the range of *burmeisterii* has a bicolored abdomen, but some specimens have an all red or all black gaster. The ocular sinus varies. In some females it is barely evident.

Males with a completely black gaster come from the provinces of Rio Negro, Buenos Aires, Entre Rios and Corrientes. Females with an all red gaster occur in the Argentine provinces of Rio Negro, Buenos Aires, Mendoza, and Tucuman as well as in Uruguay. Bicolored forms are known from all but Rio Negro and Tucuman, however.

*Distribution* (Map 6).—*Larra burmeisterii* is widespread in Argentina and Uruguay, and occurs as far south as the Rio Negro. I have a single record from Paraguay, and several from Rio Grande do Sul in southernmost Brasil. I have seen a single female labelled Santiago, Chile (VIENNA) but I presume that this is erroneous.

*Type notes.*—The holotype was destroyed by





Figs. 50-52. *Larra burmeisterii*, features of female foretibia and tarsus. 50, Outer surface of tibia. 51, Outer apex of tibia showing carina. 52, Inner surface of basitarsus.

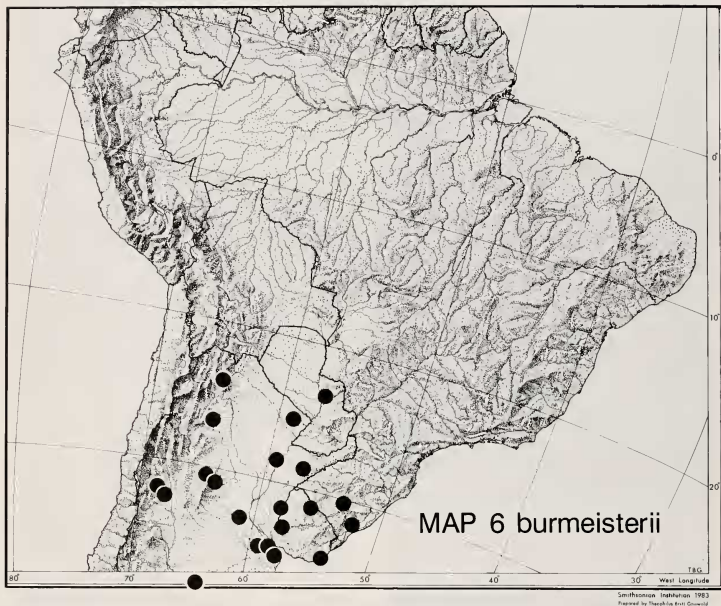
museum pests long ago, but Holmberg's (1884) description is sufficient to identify the species. The first three gastral segments were red in the type, the remainder black. This agrees with some of the females that I have seen from Uruguay. Although Holmberg used a Lynch Arribalzaga ms. name, *burmeisterii*, the description is Holmberg's. Apparently Lynch Arribalzaga was preparing a revision of the Argentine "*Larrada*" but it was never published.

#### ANALIS SPECIES GROUP

**Diagnosis.**— Placoids restricted to male flagellomeres III-VI (Figs. 13, 59-62); upper interocular distance of female less than half length of lower interocular distance (UID 0.32-0.46X LID); transverse sulcus on vertex behind ocelli usually deeply impressed at midline; vertex of female head with broad, deep sinus around eye (Figs. 4, 63-65), male with shallower sinus; female frons beneath transverse swelling polished, variably punctate, largely asetose except at level of antennal sockets, clypeus laterally, and vertex (Figs. 2, 53); inner surface of female scape largely asetose except at base (Fig. 8); female pedicel almost entirely asetose (only a few scattered setae), surface smooth, polished (Fig. 8); female mandible with poorly developed rake, setae scattered, weak (Figs. 16-17, 56, 58); labrum beveled or sloping down at apex to obtusely angular or arcuate free margin (Figs. 16-17, 55-58); pronotum anteriorly with pair of oval pits at midline that sometimes are narrowly connected; lower edge of smooth, impunctate area at outer apex of female foretibia margined below by sharp carina that extends about one-sixth tibial length (Fig. 25), male without carina; outer surface of female foretibia with row of stout spine-like setae that is occasionally closely paralleled anterad by row of several finer setae, and more distantly posterad by row of one to three stout setae (Fig. 23), male usually with single row of one to four finer setae but sometimes absent; inner surface of female forebasitarsus distad of cleaning notch with asetose linear zone that extends to apex (Fig. 28). Propodeal dorsum usually without median longitudinal carina, or with only a remnant, but occasional specimens have complete carina. Male tergum VII without pygidial carinae. Male genitalia essentially identical in all species: ventral surface of gonostyle densely covered with long setae (Fig. 128); volsellar arms straight, broadening distally, ventral surface with long setae (Fig. 129); apicodorsal crest of volsellar arm sinuate in dorsal view (Fig. 130).

**Included species.**— *Larra altamazonica* Williams, *analisis* Say, and *godmani* Cameron.

**Discussion.**— The presence of placoids on just a few of the basal male flagellomeres is an autapomorphic feature of the *analisis* group. In all other *Larra* placoids are found on flagellomeres III-XI. In the female, the combination of a polished, impunctate pedicel, the narrow upper interocular distance (less than 0.50X LID), the deep impression at the midline of the vertex, and the deep sinus around the upper eye margin, and the weak mandibular rake set the *analisis* group apart from other New World *Larra*, but of these apomorphies,



only the weak mandibular rake is unique to the group. Females of the Old World *maura* species group share the other apomorphies, but the outer face of the foretibia in that assemblage has no spine rows or an apical carina, and the labrum is flat, without an apical bevel. The female frons in the *maura* group apparently is always asetose and is essentially impunctate beneath the transverse swelling, a trait shared with one species of the *analisis* group, *altamazonica*. In the other two species of the *analisis* group, the frons, though shiny, is clearly punctate.

Species characters are few in this group. The number of flagellomeres with placoids is useful in males, but there is some intraspecific variation. Unfortunately, male genitalia seem identical in the three species. Because of this, identification of occasional males of *altamazonica* and *godmani* with atypical antennal placoid distribution can be

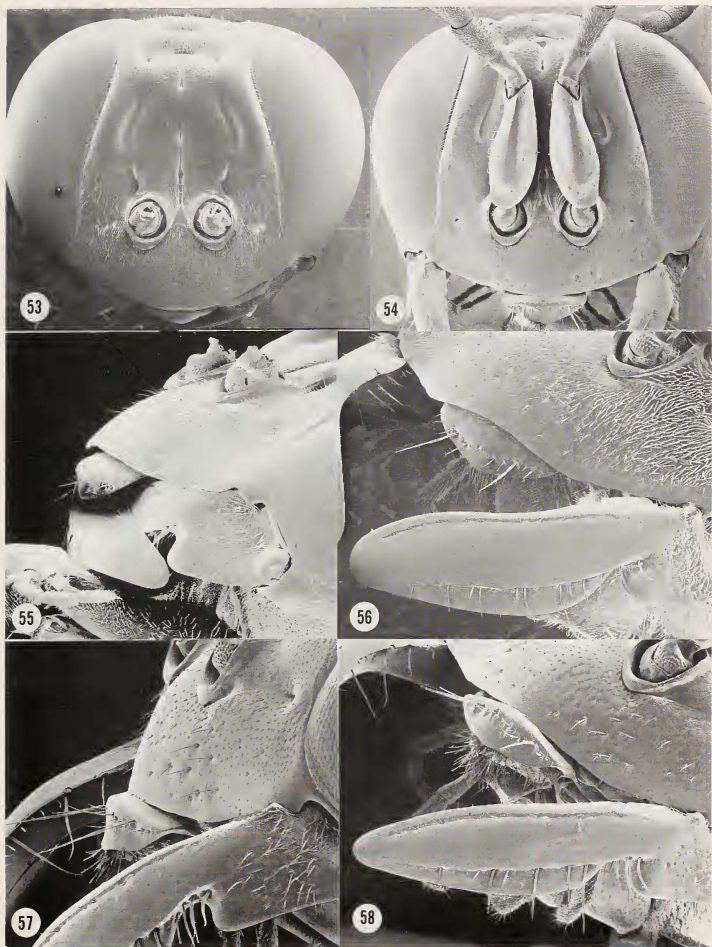
problematical. The length of the UID in relation to the LID is useful to some extent in both sexes, but there is some overlap between species. The shape of the female pygidial plate is diagnostic for *altamazonica*. Color in the *analisis* group is constant in *analisis*, but *altamazonica* and *godmani* have forms with a black gaster, and forms with a red gaster, or combinations of both.

#### *Larra analis* Fabricius

Figs. 13-14, 53, 55, 59, 63, 66, 128-131

*Larra analis* Fabricius, 1804:220. Holotype female: Carolina. (PARIS). Type studied by van der Vecht (1961:17).

*Larrada canescens* Smith, 1856:292. Holotype male ("female"): Georgia. (BMNH). Synonymy by R. Bohart (in Bohart and Menke, 1976:237).



Figs. 53-58. Female head features in *analis* group. 53-54, Face. 53, *analis*. 54, *altamazonica*. 55-58, Clypeus, labrum and mandible. 55, *analis*. 56, *godmani*. 57-58, *altamazonica*.

*Larrada americana* Cresson, 1872:214. Holotype male: Texas [presumably Bosque Co.]. (ANSP). Junior secondary homonym of *Larra americana* Saussure, 1867. Synonymy by G. Bohart (1951:953).

*Larra cressonii* Fox, 1894:482. New name for *americana* Cresson.

**Description.**— (181 males, 273 females): Male UID 0.51-0.57X LID; female UID 0.43-0.50X LID (as measured tangential to upper margin of tentorial pits); punctures of male vertex separated by about one diameter on disk, closer peripherally; female vertex punctures similar to male, but sometimes 3 or 4 diameters apart discally (Fig. 63); female frons finely punctate; placoids present on male flagellomeres III-V, and sometimes VI, lengths of placoids variable on III and VI (Figs. 13, 59); surface of labrum gradually curving down to free margin in male, more sharply beveled in female (Fig. 55); apex of female mandible narrowly rounded (Fig. 55). Pronotal pits narrowly connected. Mesopleuron dull or weakly shining. Wings evenly, darkly infumate. Propodeal dorsum usually delimited posterad by transverse carina. Male gaster black, terga sometimes with silvery apical fasciae; female gastral segments I-III black, IV-VI red. Male sternum VIII rounded at apex, often indented there; female pygidial plate narrow (Fig. 66). Male 8.5-14.5 mm long, female 12.5-18.5 mm long.

**Discussion.**—*Larra analis* is the only Nearctic species and it has a non-varying color pattern that permits easy identification. Males are all black and females have a black gaster with the last three segments red. Occasional melanic females of *godmani* from South America have the last three segments of the gaster red and thus resemble *analis*, but the UID is narrower in the latter species. The UID in melanic *godmani* ranges from 0.32-0.39X the LID, while the UID in *analis* ranges from 0.43-0.50X the LID. Males of *analis* generally have a broader UID than either *godmani* or *altamazonica*. In *analis* the UID is 0.51-0.57X the LID. In the other two species the male UID ranges from 0.35-0.50X the LID.

**Distribution** (Map 7).— Widespread in the eastern United States from about the 104th meridian to the southern and eastern coasts. Northward *analis* apparently does not extend beyond the 43rd parallel, Livingston Co. in Michigan and Taunton, Massachusetts being the northernmost records seen. The wasp is evidently uncommonly collected except in the southern tier of states.

**Type notes.**— J. van der Vecht (1961), R. Bohart (in Bohart and Menke, 1976), and G. Bohart (1951)

studied the types of *analis*, *canescens*, and *americana*, respectively, and I accept their interpretations. Cresson (1872) described *americana* from a single male which is now in Philadelphia (see Cresson, 1916). Thus the male in the U.S. National Museum of Natural History collected by Belfrage in Texas and labeled as "type" is a pseudotype.

### *Larra godmani* Cameron

Figs. 4-6, 17, 23, 25, 28, 56, 60, 64, 67

*Larrada aethiops* Smith, 1873:56. Lectotype female: "St. Paulo" (=São Paulo de Olivença, Amazonas) Brasil (BMNH), present designation. Junior primary homonym of *Larrada aethiops* Cresson, 1865.

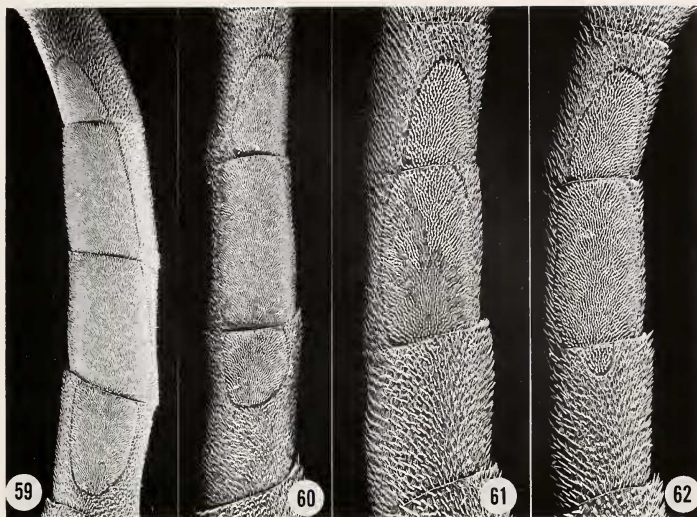
*Larra godmani* Cameron, 1889:49. Lectotype female: Orizaba, Mexico (BMNH), present designation. NEW SYNONYM.

*Larra braunsii* Kohl, 1898:351. Lectotype female: Santos, Brasil (State of São Paulo) (VIENNA), present designation. NEW SYNONYM.

*Larra transandina* Williams, 1928:56. Holotype female: Tena, Ecuador (BISHOP). NEW SYNONYM.

**Description.**— (290 males, 186 females): Male UID 0.35-0.50X LID; female UID 0.32-0.46X LID (as measured tangential to upper margin of tentorial pits); punctures of male vertex separated by less than a diameter to more than a diameter on disk, closer peripherally; female vertex irregularly punctate, punctures scattered, less than diameter apart to several diameters apart, punctures sometimes very fine, almost pinprick-like and widely separated, the vertex almost impunctate (Fig. 64); female frons finely punctate, occasionally almost impunctate; placoids typically present on male flagellomeres III-V (Fig. 60), flagellomere III rarely without placoid, placoid on III usually occupying apical half, that on V usually occupying basal two thirds or more; surface of labrum gradually curving down to free margin (Figs. 17, 56); apex of female mandible broadly rounded (Figs. 17, 56) or narrowly rounded. Pronotal pits separate. Mesopleuron usually dull or weakly shining, infrequently shiny. Wings darkly infumate, except sometimes paler at base. Propodeal dorsum sometimes delimited apically by transverse carina. Gaster all red or all black (19% of male and 17% of female specimens melanic), occasional red male specimens have tergum I suffused with black, occasional black specimens of both sexes have last two or three segments red. Male sternum VIII with apical emargination, or rounded and/or weakly





Figs. 59-62. Male flagellomeres III-V or VI showing placoids. 59, *analisis*. 60, *godmani*. 61, *altamazonica* (typical). 62, *altamazonica*.

notched. Female pygidial plate narrow (Fig. 67). Males 8-13.5 mm long, females 13-20 mm long.

**Discussion.**— The presence of placoids on male flagellomeres III-V of *godmani* differentiates the species from males of *altamazonica*. But I have seen one red gastered specimen of *godmani* without a placoid on flagellomere III (Darién, Panamá (Quintero). Positive identification of such specimens can be problematical. In the case of the Panamanian wasp, a typical male was taken at the same time and place, thus verifying its identity as *godmani*. Also it has rather dull mesothoracic pleura typical of *godmani*. I have also seen two melanic males without a placoid on flagellomere III (FSDA, MCZ) that I regard as *godmani* based on body length and rather dull mesothoracic pleura.

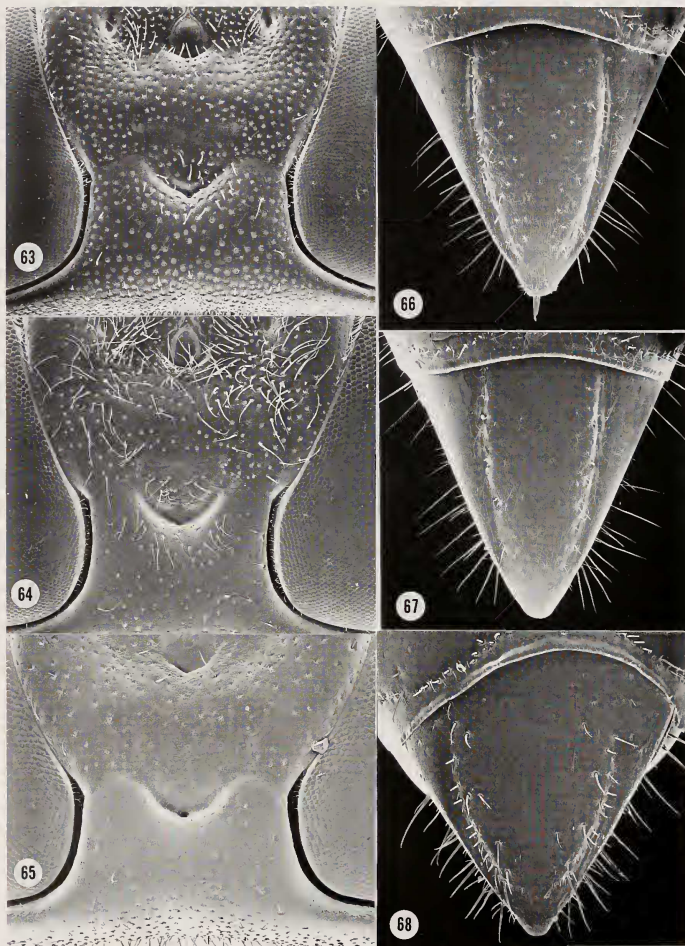
The shape of the female pygidial plate (Fig. 67) is the most reliable character for separating *godmani* from *altamazonica*. The latter species has a broader plate (Fig. 68). The frons below the transverse swelling is usually very finely punctate in females, at least in part. In *altamazonica* the female frons is

nearly impunctate or the punctures are largely effaced. The thoracic pleura of *godmani* are duller compared to *altamazonica* which tends to have shiny pleura.

Males of *godmani* with an all red gaster are quickly separated from males of *analisis*, all of which have a black gaster. The narrower male UID of *godmani*, especially those with an all black gaster, generally distinguishes this sex from *analisis*. The UID ranges from 0.35-0.43X the LID in black males of *godmani*, while in *analisis* the range is 0.51-0.57.

Females with a red gaster are easily separated from *analisis*, but the occasional melanic *godmani* with the terminal segments red must be identified by measuring the upper interocular distance. In melanic *godmani* the UID ranges from 0.32-0.39X the LID; in *analisis* the UID is 0.43-0.50X the LID. Of course the two species are allopatric. In about half of the *godmani* females studied, the apex of the mandible is more broadly rounded than in *analisis* or *altamazonica* (compare Figs. 56, 58), but in all material studied from Mexico, the northern end of the





Figs. 63-68. Female features of *analis* group. 63-65, Vertex of head. 63, *analis*. 64, *godmani*. 65, *altamazonica*. 66-68, Pygidial plate. 66, *analis*. 67, *godmani*. 68, *altamazonica*.

species' range, the mandible is more or less narrowly rounded apically.

All black males represent about 20% of my material, but all specimens from Central America and Mexico have a red gaster. Black males occur randomly in South America north of the Tropic of Capricorn. I have seen only one melanic male from south of the 23rd parallel, and it is an old specimen labeled "Montevid.", presumably Montevideo, Uruguay (BERLIN). Occasional black males from Colombia, Ecuador, Peru and northern Brasil have the last two or three gastral segments red.

All black females occur less frequently (17%) than males but like them all are from South America. They occur randomly from Venezuela down to Bolivia, and Mato Grosso, Brasil, and along the Amazon River in Brasil. I have not seen melanic females south of the 18th parallel, nor from Trinidad and the Guiana's. I have seen red tipped black females from Venezuela, Colombia, Ecuador and Pará, Brasil. The upper interocular distance in melanic females tends to be narrower than in bicolored ones. The UID ranges from 0.32-0.39X the LID in melanics, and between 0.33-0.46 in bicolored females.

I have one small female from Leticia, Colombia (FSDA) that I have identified as *godmani*; it is only 9 mm long. It has a narrow pygidial plate, but the pleura are shiny like *altamazonica*. Its UID is 0.44X the LID which is beyond the range of female *altamazonica*.

**Distribution** (Map 8).—Widely distributed in the Neotropical Region, ranging from just south of the Tropic of Cancer in Mexico to extreme northern Argentina, Paraguay, southeastern Brasil and Uruguay. Bolivian material of *godmani* was liberated in Alachua Co., Florida in 1988-89 under the name *braunsii* (Bennett et al., 1990), but the species apparently did not establish.

**Type notes**.—Smith described *aethiops* from an unspecified number of females from "St. Paulo" and "Ega", Brasil that had a black gaster. I have examined four syntypes, one labelled St. Paulo and three labelled Ega (BMNH, OXFORD). I have selected the São Paulo de Olivença female as lectotype and so labelled it. The mandible apex is broadly rounded in the four specimens, and the UID is 0.34X the LID in the lectotype.

Cameron had at least two red abdomened females from Orizaba, Mexico when he described *godmani*. I have studied two from the BMNH and placed a lectotype label on the best specimen (its gaster is glued to a card). The mandible apex is not broadly rounded in either specimen. The UID is 0.36X the LID in the lectotype.

Kohl described *braunsii* from three female syntypes (VIENNA) with a red gaster. I have studied them and selected the specimen from Santos, Brasil as lectotype. Only the Pebas, Peru ("Pevas") syntype has the mandible apex broadly rounded. The UID is 0.40X the LID in the lectotype.

Williams female holotype of *transandina* has a red gaster, the mandible apex is broadly rounded and the UID is 0.38X the LID.

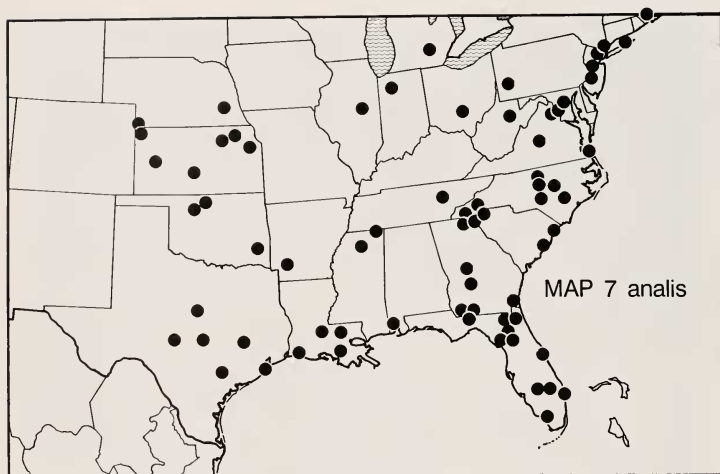
#### *Larra altamazonica* Williams

Figs. 2, 8, 16, 54, 57-58, 61-62, 65, 68

*Larra altamazonica* Williams, 1928:57. Holotype female: Tena, Ecuador (BISHOP).

**Description**.—(42 males, 50 females): Male UID 0.40-0.49X LID, female UID 0.37-0.41X LID (as measured tangential to upper margin of tentorial pits); punctures of male vertex separated by less than diameter to two or three diameters on disk, denser peripherally; female vertex punctures often pin prick-like, punctation usually absent laterally, punctures sparse on disk, usually several diameters apart, disk sometimes nearly impunctate (Fig. 65); female frons beneath transverse swelling almost impunctate (Fig. 2); placoids typically present only on male flagellomeres IV-V, flagellomere III occasionally with small placoid apically (Figs. 61-62); surface of labrum rather abruptly angled down to free margin (Figs. 16, 57-58); apex of female mandible narrowly rounded (Fig. 58). Pronotal pits separate. Mesopleuron usually shiny. Wings weakly to moderately infumate except often clear basally, wings sometimes almost entirely clear in male. Apex of propodeal dorsum sometimes delimited by short transverse carina. Gaster usually black in male, rarely reddish basally; female gaster all red or all black (30% of specimens), occasionally with last two to four segments red. Male sternum VIII usually rounded apically, sometimes truncate or even weakly notched. Female pygidial plate broad (Fig. 68). Males 7-11.5 mm long, females 7-13.5 mm long.

**Discussion**.—This is the smallest species of *Larra* in the New World, and it is separated from *godmani*, its most similar relative, by the broad female pygidial plate (Fig. 68), and in the male by the presence, in most specimens, of placoids only on flagellomeres IV-V of the antenna (Fig. 61). The abrupt apical declivity of the labrum (Figs. 57-58), and typically polished mesopleuron are additional recognition features, but neither are wholly reliable for separation from *godmani*. In the female the sparse



punctuation of the vertex (Fig. 65) and almost impunctate frons, are distinctive, but some specimens of *godmani* are similar. Occasional males have a small placoid at the apex of flagellomere III (Fig. 62), and of course, a few males of *godmani* have placoids only on IV-V instead of the normal III-V. Association with females may be the only way to identify such males, and even then it is only presumptive. Male sternum VIII is most often rounded in *altamazonica* but in *godmani* is most often notched there.

The occurrence of melanic females in *altamazonica* is apparently higher than in *godmani* with one third of my material having a black gaster or black with the apical segments red. These seem to occur randomly in the western Amazonian Basin. I have two males in which gastral segments I-II are red and the rest are blackish. These are from Trinidad and Guyana, and are the only males of *altamazonica* that I have from these countries. Within the *analis* group this particular color pattern is unique to *altamazonica*.

**Distribution (Map 9).**—Venezuela, Trinidad, the Guianas, and apparently widely distributed in the Amazonian Basin although most records are from its western fringe. Not known south of the 18th parallel.

**Type notes.**—Williams' holotype and paratypes have been examined. The type has a red gaster.

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David Wahl, American Entomological Institute, Gainesville, Florida, graciously offered to phylogenetically analyze the species groups of *Larra* and related genera for me; I sent him my data matrix and he ran it in Hennig86. Dave also provided me with the cladogram and consensus tree presented here, and I am especially grateful for his help. Fred Bennett, University of Florida, Gainesville, Florida, sent me copies of rearing records for several generations of *Larra bicolor* and *praedatrix* so that I could identify offspring and correlate males with females. Woj Pulawski, California Academy of Sciences, San Francisco, California offered his insight into various problems that we discussed at length over the telephone. James Carpenter, American Museum of Natural History, New York, and David Wahl critically reviewed the entire manuscript. Eric Grissell, Douglas Ferguson, and Dave Nickle, Systematic Entomology Laboratory, USDA, Washington D.C. reviewed portions of the manuscript; Eric, and other members of the Ashmead Club, graciously put up with my many complaints about how awful *Larra* was as a research problem.

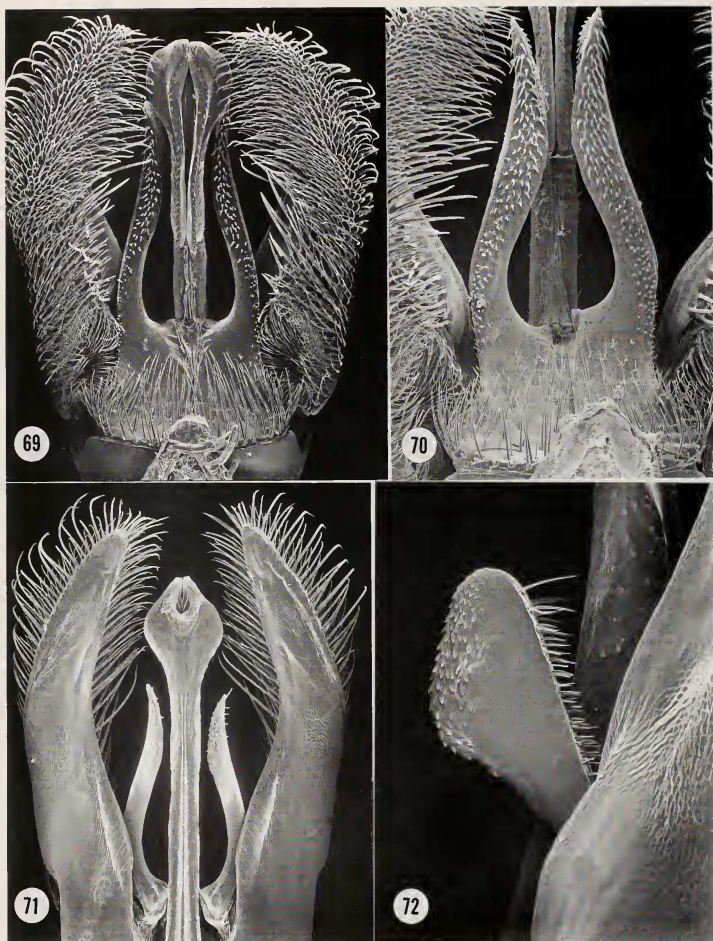




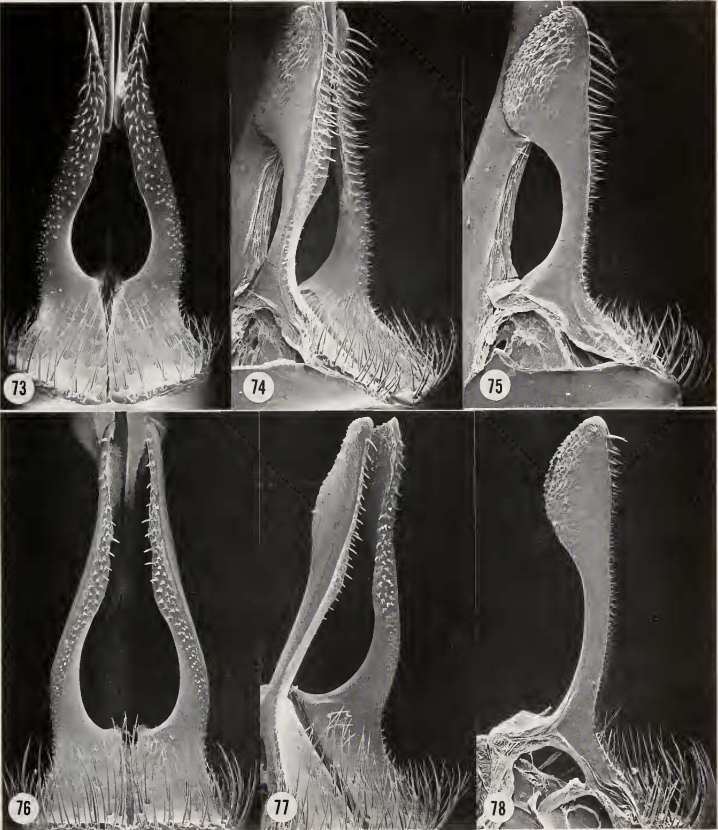


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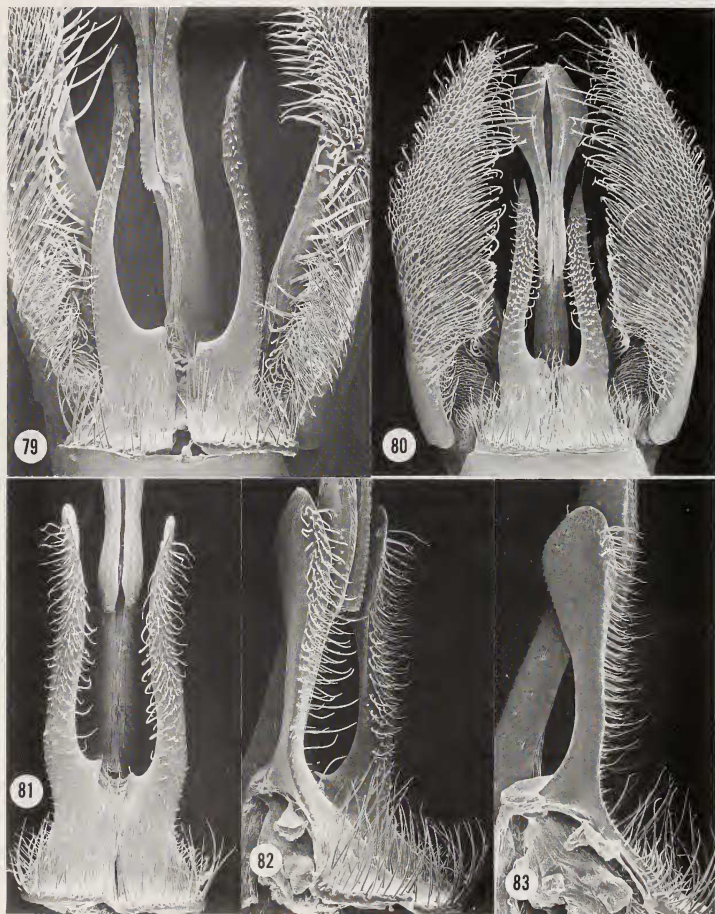
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Figs. 69-72. Male genitalia of *bicolor*, specimen from Buena Vista, Bolivia. 69, Ventral view. 70, Ventral view of volsella. 71, Dorsal view. 72, Lateral view of apicodorsal crest of volsellar arm.

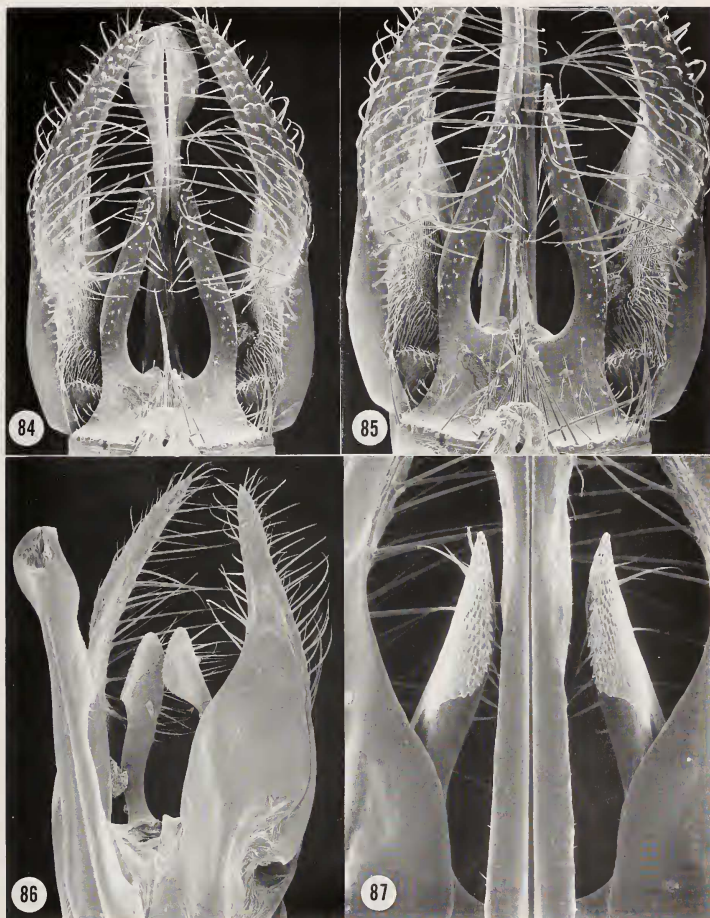


Figs. 73-78. Volsella of male genitalia of *bicolor*. 73-75, Ventral, oblique, and lateral views, respectively of specimen from Saavedra, Bolivia. 76-78, Ventral, oblique and lateral views, respectively of specimen from El Tucuco, Venezuela.



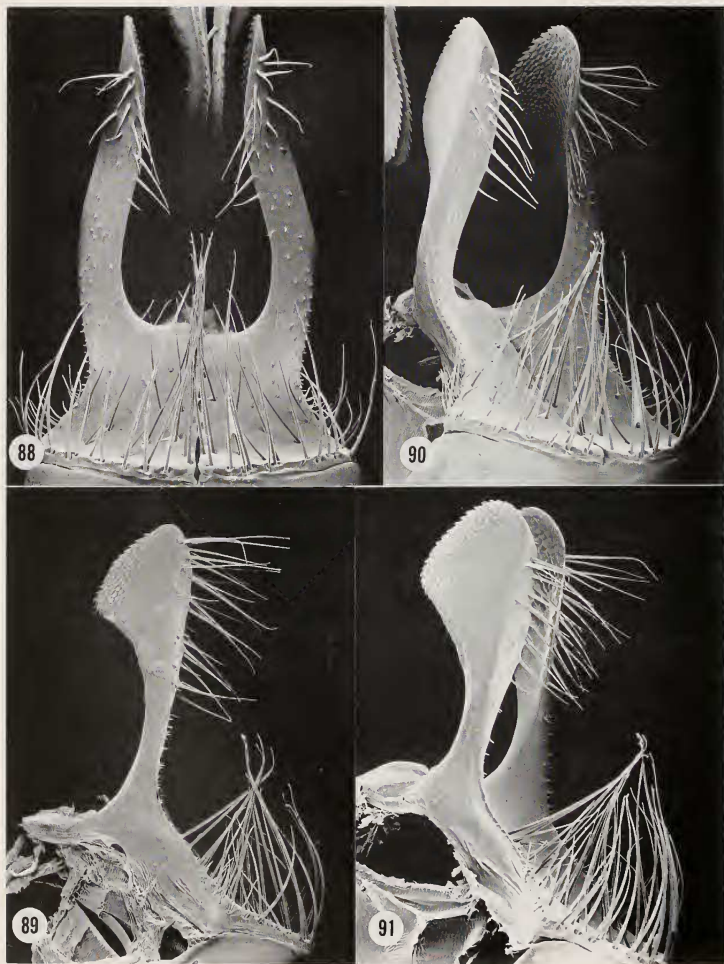
Figs. 79-83. Male genitalia of *bicolor* group. 79, Ventral view of volsella of *bicolor* from Saavedra, Bolivia. 80-83, Venezuelan population of uncertain status in *bicolor* complex. 80, Ventral view of genitalia of specimen from Hato Masaguaral. 81-83, Ventral, oblique and lateral views, respectively, of volsella of specimen from El Limon.



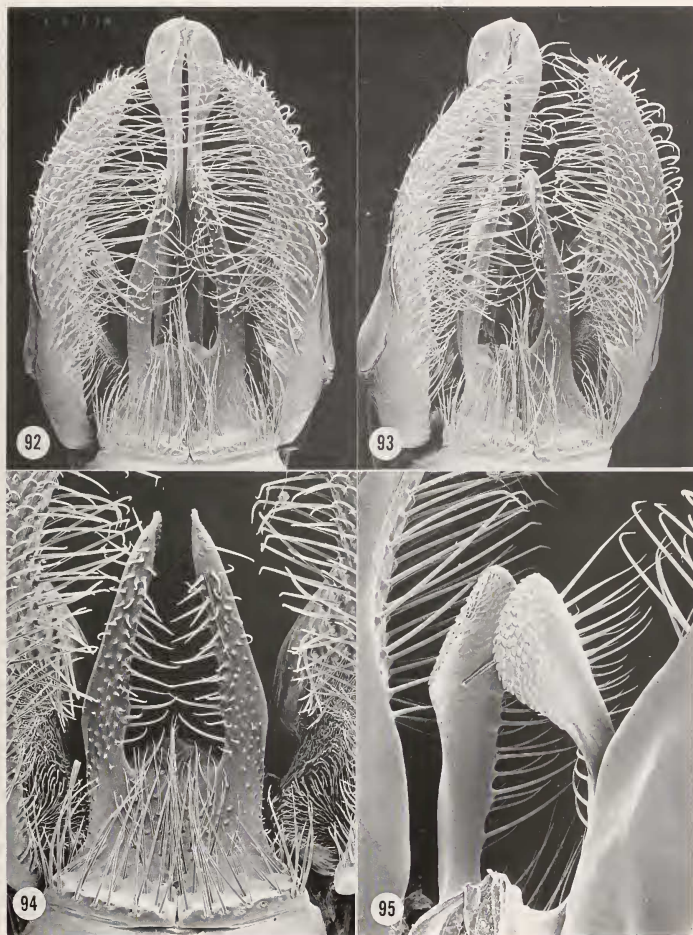


Figs. 84-87. Male genitalia of *praedatrix* from Saavedra, Bolivia (compared and identical with holotype). 84, Ventral view. 85, Ventral view of volsella. 86, Oblique dorsal view. 87, Dorsal view showing apex of volsellar arms.

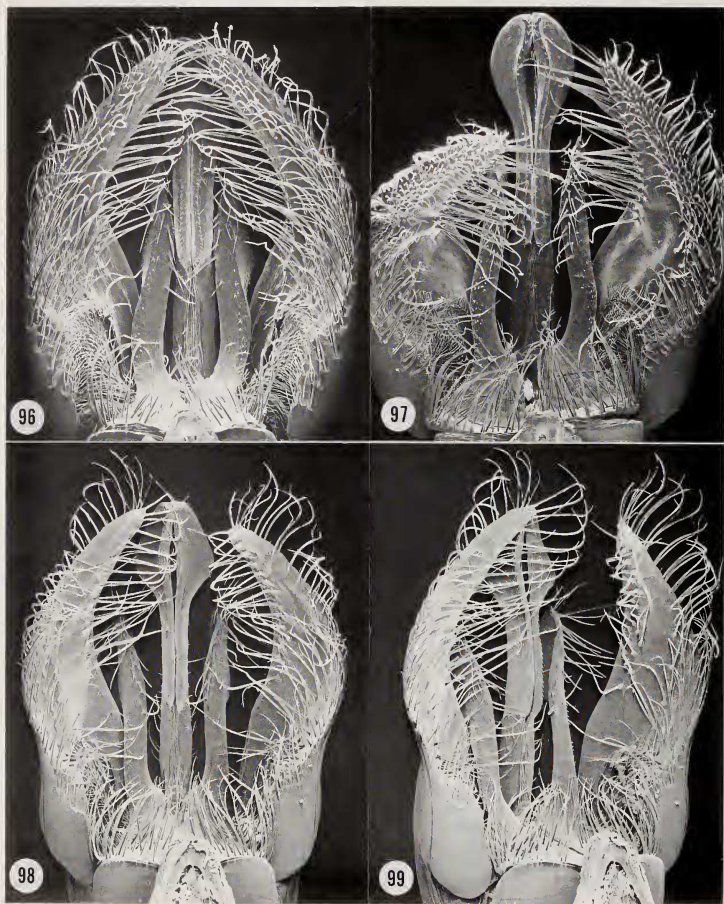




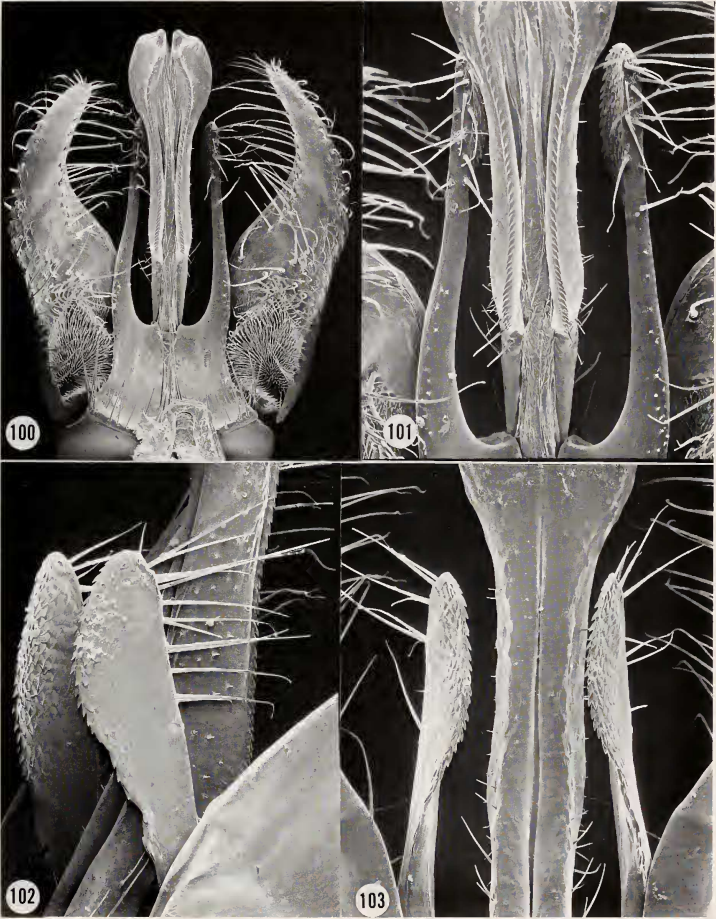
Figs. 88-91. Volsella of male genitalia of *praedatrix* from Saavedra, Bolivia; ventral, lateral and two oblique views, respectively.



Figs. 92-95. Male genitalia of *praedatrix*. 92-93, Ventral and oblique ventral views, respectively, of specimen from Caaguazu, Paraguay. 94-95, Specimen from Belém, Brasil. 94, Ventral view of volsella showing extension of long apical setae to base of arm along inner margin. 95, Oblique dorsal view of volsellar arms showing long setae to base of arm.

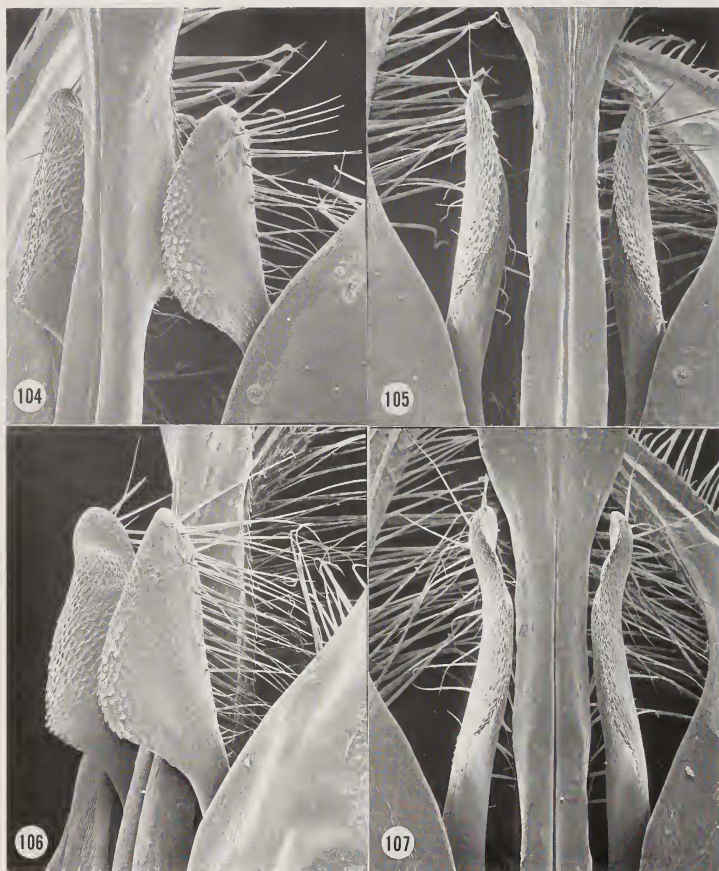


Figs. 96-99. Ventral views of male genitalia of *praedatrix*. 96, Specimen from El Salvador. 97, Specimen from Buenos Aires, Argentina. 98-99, Specimen from Costa Rica.



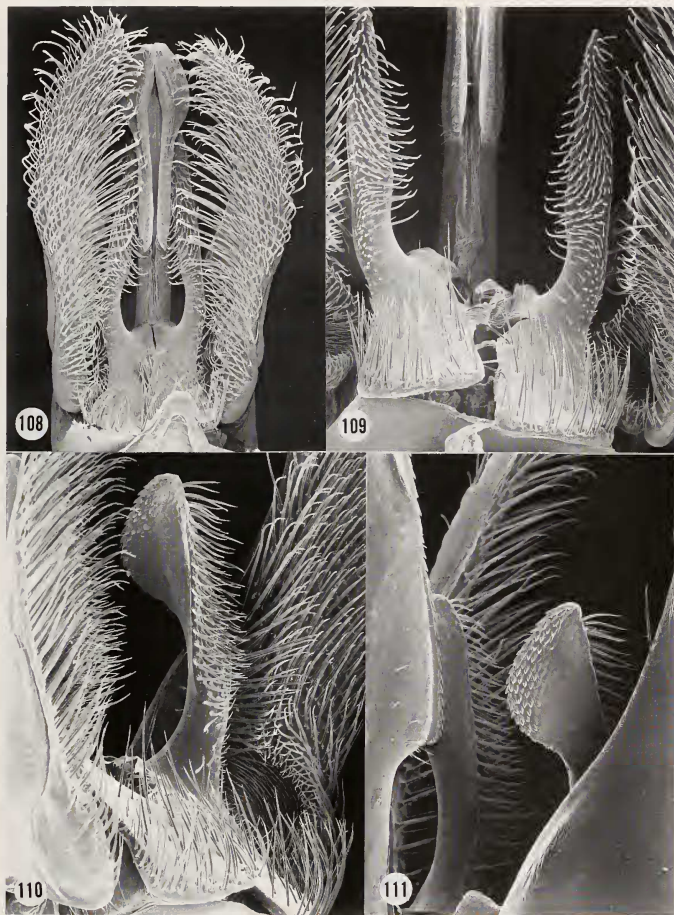
Figs. 100-103. Male genitalia of specimen of *praedatrix* from San Pedro, Paraguay showing largely asetose gonostyle and straight, narrow volsellar arms. 100, Ventral view. 101, Ventral view of volsella. 102, Oblique dorsal view of apex of volsellar arms. 103, Dorsal view of volsellar arms.



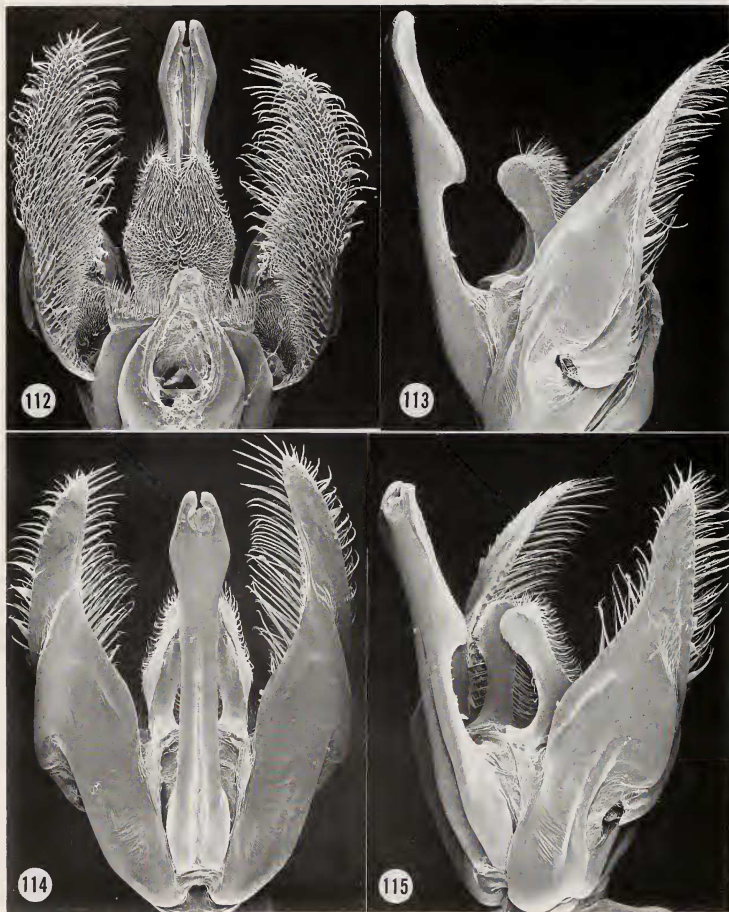


Figs. 104-107. Laterodorsal and dorsal views, respectively, of volsellar apices of *praedatrix*, specimens from Buenos Aires, Argentina. 104-105, Same specimen illustrated by Fig. 97. 106-107, Different specimen.

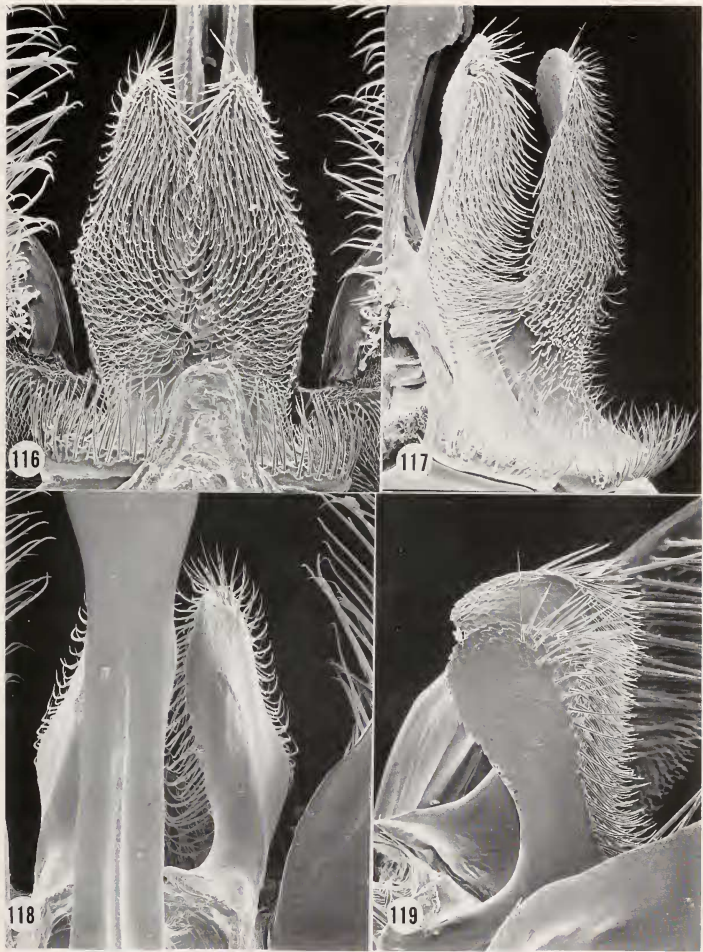




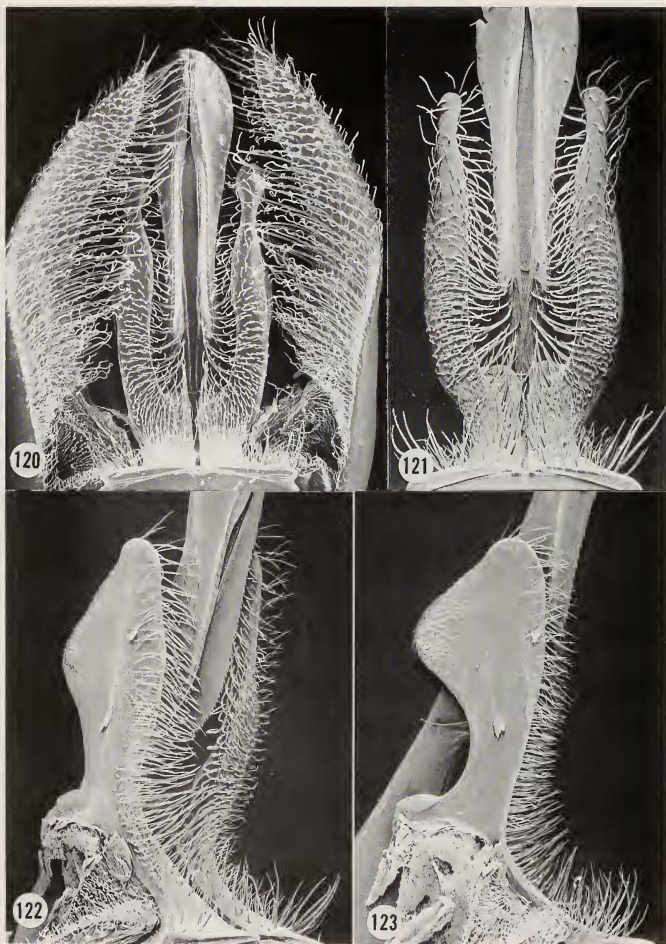
Figs. 108-111. Male genitalia of *stangei*. 108, Ventral view (specimen from Salta, Argentina). 109, Ventral view of volsella of specimen from El Palmar, Bolivia (left and right halves disassociated). 110, Oblique ventral view of volsella of same specimen. 111, Dorsolateral view of apex of volsella of same specimen.



Figs. 112-115. Male genitalia of *princeps*. 112, Ventral view. 113, Lateral view. 114, Dorsal view. 115, Dorsolateral view.

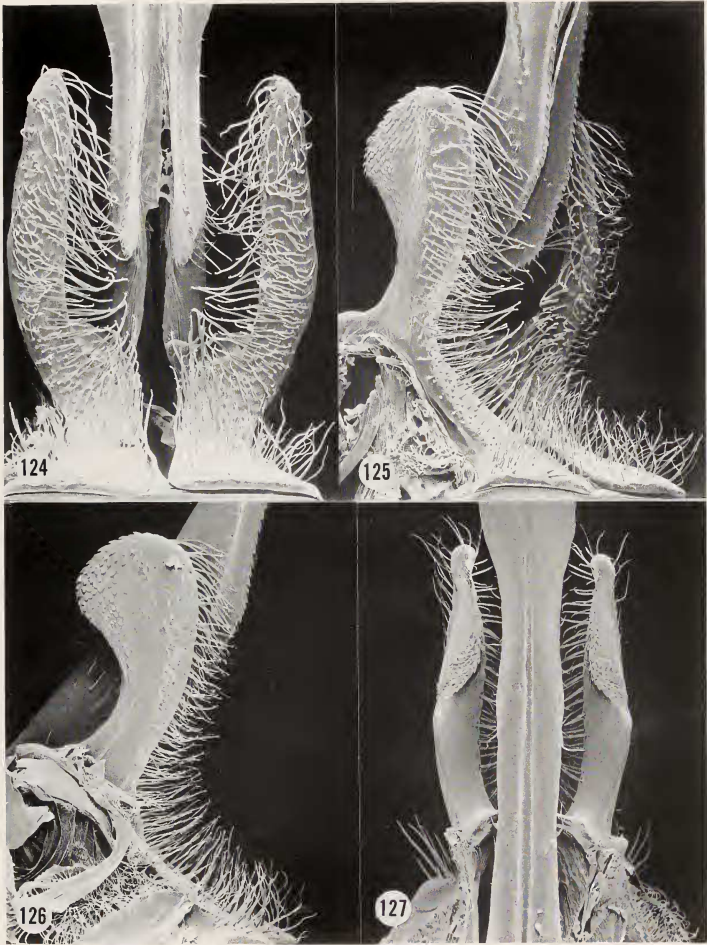


Figs. 116-119. Details of male genitalia of *princeps*. 116, Ventral view of volsella. 117, Oblique ventral view of volsella. 118, Dorsal view of volsellar apex. 119, Lateral view of volsellar apex.



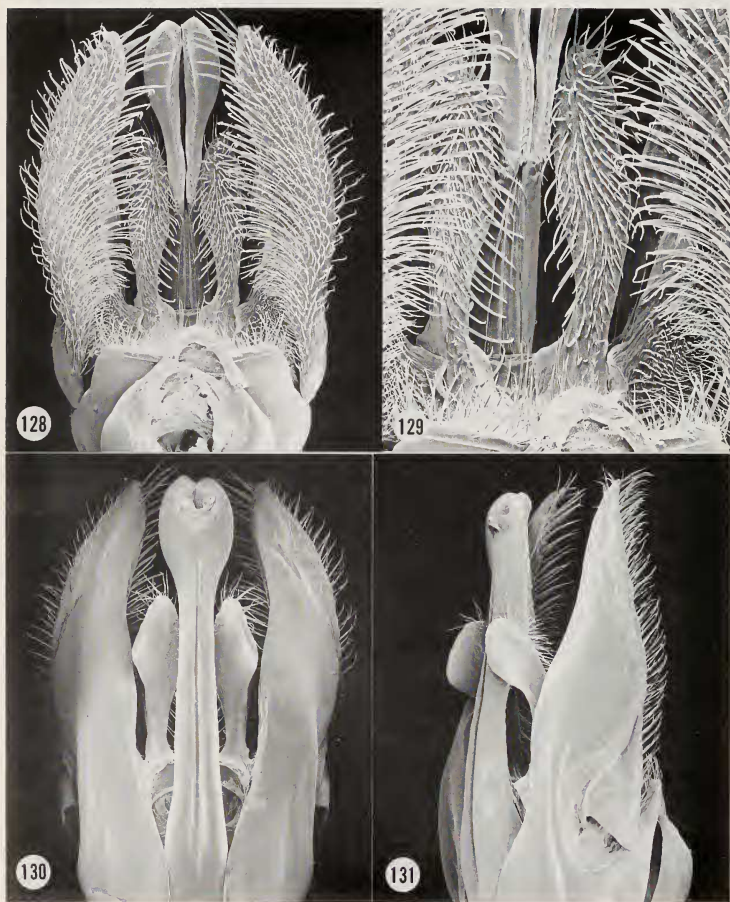
Figs. 120-123. Male genitalia of *burmeisterii* (specimens from Entre Rios, Argentina). 120, Ventral view. 121, Ventral view of volsella. 122, Oblique ventral view of volsella. 123, Lateral view of volsella.





Figs. 124-127. Volsellar details of male genitalia of *burmeisterii* (specimen from Montevideo, Uruguay). 124, Ventral view. 125, Oblique ventral view. 126, Lateral view. 127, Dorsal view.





Figs. 128-131. Male genitalia of *analis*. 128, Ventral view. 129, Ventral view of volsella. 130, Dorsal view. 131, Oblique lateral view.